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GENETIC IMPROVEMENT OF LEAN MEAT PRODUCTION  
IN TERMINAL SIRE BREEDS OF SHEEP

N.D. CAMERON, B.Sc., M.Sc.

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

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To Vicky

## TABLE OF CONTENTS

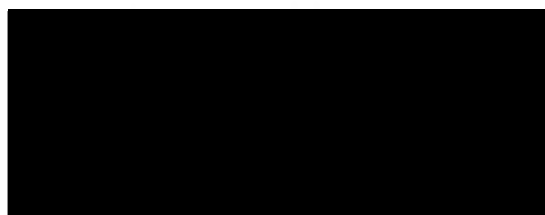
	Page
DECLARATION	i
ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
INTRODUCTION	v
CHAPTER 1. GENETIC IMPROVEMENT OF LEAN MEAT PRODUCTION IN TERMINAL SIRE BREEDS OF SHEEP : A REVIEW	
Introduction	1
Sheepmeat production in Britain	2
Between-breed selection	3
Within-breed selection objectives	4
Genetic and phenotypic parameters	8
Selection objectives and criteria	12
Results from selection experiments	14
Genetic variation in physiological traits	16
Summary	17
CHAPTER 2. COMPARISON OF TERMINAL SIRE BREEDS FOR GROWTH AND CARCASS TRAITS IN CROSSBRED LAMBS	
Introduction	18
Materials and Methods	18
Results	22
Discussion	31
Summary	35
CHAPTER 3. RESPONSES IN LAMB PERFORMANCE FROM SELECTION ON SIRE 100-DAY WEIGHT	
Introduction	36
Materials and Methods	36
Results	40
Discussion	44
Summary	51
CHAPTER 4. ESTIMATION OF CARCASS LEANNESS IN YOUNG RAMS	
Introduction	52
Materials and Methods	54
Results	56
Discussion	62
Summary	65
Appendix	66



	Page
CHAPTER 5.	DESIGN OF MULTIVARIATE SELECTION EXPERIMENTS TO ESTIMATE GENETIC PARAMETERS
	Introduction 67
	Optimality criteria 68
	Standardisation of traits 69
	Estimation and design from response to divergent truncation selection 70
	Estimation and design from offspring-parent regression 76
	Elliptical selection experimental design 83
	Optimising the selection proportion, the family size and the ratio of individuals measured in the two generations 87
	Extensions 92
	An example 93
	Summary 96
	Appendices 97
CHAPTER 6.	GENETIC RELATIONSHIPS BETWEEN GROWTH AND FOOD INTAKE IN PERFORMANCE TESTED RAM LAMBS : AN INVESTIGATION OF GENETIC VARIANCE COMPONENT ESTIMATION PROCEDURES
	Introduction 100
	Materials and Methods 101
	Results 106
	Discussion 114
	Summary 120
CHAPTER 7.	GENERAL DISCUSSION AND CONCLUSIONS 121
REFERENCES	127
PUBLICATIONS	135

## DECLARATION

I declare that this thesis is my own composition and reports analysis of data done by me. The data were collected by members of staff of the AFRC Institute of Animal Physiology and Genetics Research (Edinburgh). The experiments analysed in Chapters 2, 3 and 4 were initiated and supervised by Prof. C. Smith. R. Thompson suggested the concept of selection on an ellipse and derived several of the formulae in Chapter 5.



N.D. CAMERON  
University of Edinburgh  
September, 1987.

## ABSTRACT

Several aspects of genetic improvement of lean meat production in terminal sire breeds of sheep were examined.

A comparison of six terminal sire breeds for lamb production traits linked results from previous studies and concluded that a first approximation to the performance of a terminal sire breed may be obtained from knowledge of its mature weight.

The response to selection on weight at fixed age of artificially reared rams was evaluated. Crossbred progeny from high and low selected rams were compared for production traits, but no real differences were found between the high and low groups. The genetic correlation between performance under artificial and natural rearing was markedly less than one.

Methods for estimating body composition in the live animal were compared. Ultrasonic backfat and muscle measurements, non-esterified fatty acids and very low density lipoprotein plasma concentrations and food efficiency measurements were tested as predictors of carcass lean proportion. Only the ultrasonic measurements were potentially useful in a breeding programme for the efficient production of lean meat.

The genetic relationships between growth and food intake were estimated using data on performance tested ram lambs. The heritability of food intake (0.70) was higher than the heritability of log (food conversion ratio) (0.08). The genetic correlations between food intake, log FCR and average daily gain were at least 0.9.

The design of multivariate selection experiments to estimate genetic parameters was developed due to the need for precise estimates of genetic parameters for growth and carcass traits. The selection criterion developed was to select individuals as parents using an index of the sums of squares and crossproducts of the phenotypic measurements.

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The data analysed in this thesis was obtained from sheep research projects which were initiated and supervised by Charlie Smith. I am grateful that he gave me the opportunity to analyse this data and for the experience and motivation I gained through working with him.

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## INTRODUCTION

The efficiency of lean meat production in the sheep industry can be increased through genetic improvement of the terminal sire breeds providing particular information is available. Given a production system, what is the appropriate terminal sire breed to use? What traits should be selected for within a breed? How can breeding values for carcass traits be estimated for the live animal? What combination of traits selected on will optimise the efficiency of lean meat production? Currently, the answers to these questions are vague and subjective, as there is little reliable information available on lean meat production traits both between and within the terminal sire breeds.

This thesis provides information to answer some of these questions and suggests methods by which answers may be obtained. Initially, genetic improvement of lean meat production in terminal sire breeds of sheep is reviewed. The experimental part of the thesis is in five separate chapters

- 1) comparison of terminal sire breeds for growth and carcass traits with their progeny slaughtered on various criteria
- 2) examination of the responses in growth and carcass traits to selection for growth rate
- 3) study of methods for estimating carcass traits in the live animal to enable selection for carcass traits
- 4) the design of multivariate selection experiments to estimate genetic parameters was initiated from the need to obtain precise estimates of genetic parameters for growth and carcass traits

- 5) estimation of the genetic relationships between growth and food intake in performance tested ram lambs to quantify the genetic variation in food efficiency

## CHAPTER 1

### GENETIC IMPROVEMENT OF LEAN MEAT PRODUCTION IN TERMINAL SIRE BREEDS OF SHEEP

#### Introduction

The Meat and Livestock Commission estimated that approximately 20% of total carcass weight in sheep was waste fat for sheep slaughtered in 1984, assuming that a lean : fat ratio of 5 : 1 was desirable to the consumer (Kempster, Cook and Grantley Smith, 1984). The comparable percentages for waste fat in cattle and pigs were 22% and 12% respectively. Expenditure and consumption of lamb has declined by 37% since 1970, allowing for inflation rate (Meat and Livestock Commission (MLC), 1986). The production of waste fat is inefficient in terms of the energy resource expended in production of excess fat (Webster, 1977) and undesirable due to the effect excessive fat has on consumer consumption (Nute, Francombe and Dransfield, 1983). In biological and economic terms, the efficiency of lean meat production in sheep would be increased if waste fat in the carcass was decreased.

The main reason for the failure of the sheep industry to meet the consumer demand for leaner meat has been a financial one. The Sheep Variable Premium payment scheme, which accounted for 22% of producers' total returns in 1985 (MLC, 1986), has reduced the effect of decreased consumer demand for lamb. Since January 1986, lambs in fat classes 4H and 5 of the MLC Sheep Carcass Classification Scheme were ineligible for the Sheep Variable Premium. In 1984 and 1985 less than 5% of all classified carcasses were in these fat classes (MLC, 1986), such that restricted payment



of the Sheep Variable Premium will have a negligible effect in creating an incentive to produce leaner carcasses. Another reason for the lack of response to consumer demand is that 70% of lambs sold live have no subsequent carcass information which could be useful to the producer (MLC, 1986).

There are two factors which may provide real financial incentives for improved production of lamb. Changes in New Zealand's agricultural and export policies would have important consequences on the British sheep industry as the majority of imported lamb comes from New Zealand (97%) and it accounts for approximately 40% of British sheepmeat consumption (MLC, 1986). If the amount of imported lamb from New Zealand decreased significantly, then British lamb would take a greater share of the market which may further reduce lamb consumption as the retail price of British lamb is 1.3 times higher than New Zealand lamb (MLC, 1986). Secondly, the European Economic Community Sheepmeat Regime is to be reviewed before October 1988 and as Britain is the main beneficiary, then the Sheep Variable Premium may be closely examined. These two factors may be the real financial incentives for the sheep industry to improve lean meat production as required by both the industry and consumer.

#### Sheepmeat production in Britain

300,000 tonnes of sheepmeat was produced in Britain during 1985 of which 63% was produced from lowland flocks (MLC, 1986). The majority of lambs from lowland flocks are sired by rams from terminal sire breeds. Approximately 30% of the genes of slaughtered

lambs are from terminal sire breeds and purebred ewes of these breeds account for only 5% of the British breeding sheep population (MLC, 1972). Genetic improvement of lean meat production in terminal sire breeds is sensible as firstly, between and within breed selection can be concentrated on a numerically small group of animals which have a large effect on sheepmeat production, and secondly, selection can be concentrated on production traits as a negligible number of crossbred progeny from terminal sire breeds are retained for breeding.

#### Between breed selection

The performance of various terminal sire breeds for growth and carcass traits has been compared (Wolf, Smith and Sales, 1980, Kempster, Croston, Guy and Jones, 1987). The slaughter criteria were slaughter at fixed weight or at an equal estimated level of fat cover. Differences in growth and carcass traits between breeds could be accounted for by differences in mature weight, even with the two slaughter criteria. In general, the ranking of the terminal sire breeds for lean growth rate was essentially consistent with the ranking for mature weight for slaughter at fixed weight (Wolf et al, 1980). Breeds of a heavy mature weight took longer to reach a particular level of fat cover, which resulted in heavier carcasses, than breeds of light mature weight (Kempster et al, 1987). These results suggest that a first estimate of a terminal sire breed's performance may be obtained from knowledge of its mature weight.

Deviations from these first estimates are expected, such as the Texel breed which has a lower growth rate and higher carcass lean proportion than would be predicted from its mature weight (Wolf

et al, 1980). The slower growth rate of the Texel breed may reduce its advantage of high lean proportion due to the Guide Prices of the European Economic Community Sheepmeat Regime. The reduction of the Guide Prices in late summer implies a disadvantage to breeds which reach market requirements later than other breeds (Kempster et al, 1987). Unless a premium for carcass lean proportion was available, then use of the Texel in lamb production may not be desirable.

#### Within-breed selection objectives

Traits which ideally should be considered in the selection objective of a terminal sire include carcass traits, food intake and lamb survival (Ponzoni, 1982; Atkins, 1987), as these are traits which are directly concerned with lean meat production. Carcass weight, lean weight and proportion may be the carcass traits to be maximised while fat weight and proportion need to be reduced.

With selection for reduced carcass fat, account should be taken of fat distribution for ease of trimming. The heritability estimates for the proportion of subcutaneous, intermuscular and internal fat in the carcass were similar; 0.36, 0.37 and 0.36 respectively (Wolf et al, 1981), which suggests considerable genetic variation in fat deposition within fat depots. However, the genetic correlations between fat depots were less than 0.7. Although total carcass fat can be reduced through selection, correlated responses in the various fat depots will not be similar. The genetic parameter estimates are currently not sufficiently precise that fat distribution could be effectively included in the selection objective.

Another aspect of fat distribution is the relative amount of inter- and intra-muscular fat in the carcass. Intra-muscular fat may be associated with eating quality of meat (Wood, 1984) and selection for reduced carcass fat content may result in lower levels of intra-muscular fat. Dransfield, Nute, MacDougall and Rhodes (1979) found no sire breed effect on the eating quality of lamb for several sire breeds, including the Texel. A more important factor of lamb eating quality was toughness, caused by the rate of chilling, (Dransfield et al, 1979) which was less severe in fatter lambs due to the insulating effect of subcutaneous fat cover.

Carcass traits are difficult to measure in the live animal, but they can be included in the selection objective without being included in the selection criterion. Several indirect methods of predicting carcass composition include conformation (Kempster, Croston and Jones, 1981), ultrasonic measurements (Simm, 1987) and computer tomography (Sehested, 1984). Economic weights for carcass traits are difficult to assess due to the existing marketing system, although Parratt and Simm (1987) have derived some figures, on a national basis, for growth rate, dressing and carcass lean proportions.

James (1982) recommended that the selection objective should include food intake unless there was no genetic variation in food intake which was independent of growth rate. Food intake was not included in the selection objective of Parratt and Simm (1987) as their model assumed that lean growth rate was genetically uncorrelated with food conversion efficiency. Clearly, there is a need for more information on the genetic parameters of food intake

and production traits.

Lamb survival has a low heritability (Cundiff, Gregory and Koch, 1982) but may have a negative genetic correlation with birth weight (Bradford and Meyer, 1986). The difference between a selection objective which increases lamb survival with one which restricts the genetic change of birth weight on overall lean meat production can only be determined when precise estimates of the appropriate genetic parameters are available.

Given that lambs are slaughtered at fixed age or weight according to market preference, that the economic weights for traits in the selection objective are poorly specified and that the appropriate genetic and phenotypic parameters are either unknown or imprecisely estimated, then in the short term realistic selection objectives may only include growth rate and a component of carcass composition. In the long term, the selection objective may include other traits but only when more information is available.

Various possible selection objectives have been examined by several authors to determine the objective which would result in maximum genetic improvement in lean meat production. The selection objectives were generally to improve a combination of traits, e.g. lean growth rate, or several traits combined in an index. The various selection objectives and selection criteria which were examined are included in Table 1.1. Each of the authors used their own parameter set for comparing the effectiveness of the selection criteria, due to the lack of reliable estimates of the appropriate parameters. A comparison of the selection objectives for genetic improvement of lean meat production and of the effectiveness of the

TABLE 1.1

Selection objectives and criteria for genetic improvement  
of lean meat production in sheep

Selection objective	Traits in selection criterion	Author
lean growth rate or carcass fat proportion	individual W UBF (individual and half-sib) W UBF  individual W and half-sib CW CBF  individual W and progeny CW CBF	B
lean growth	W adjusted for age and UBF adjusted for weight	P
carcass weight and carcass backfat depth (economic weights)	W UBF W UBF : restricted index on CBF W UBF : restricted index on CW W UBF adjusted for weight	R
growth rate, dressing and lean proportion (economic weights)	W UBF	Pa
carcass lean and fat weights (desired gains index)	W UBF UMD	Si
carcass lean and fat weights (economic weights)	W UBF UMD	S

W : liveweight at constant age  
 UBF : ultrasonic backfat depth  
 CBF : carcass subcutaneous fat depth  
 CW : carcass weight  
 UMD : ultrasonic muscle depth

B : Bennett and Clarke, 1984  
 P : Purchas, Bennett and Dodd, 1975  
 R : Rae, 1984  
 Pa : Parratt and Smith, 1987  
 Si : Simm and Dingwall, 1987  
 S : Simm, 1986

various selection criteria can only be made if the same parameter set is used in all comparisons.

#### Genetic and phenotypic parameters

There are only two reports of genetic and phenotypic parameters for several growth and carcass traits in the literature, namely Parratt, Burt, Bennett, Clarke, Kirton and Rae (1987) and Wolf, Smith, King and Nicholson (1981). The slaughter criterion of the Parratt study was not defined but parameter estimates were obtained for slaughter at fixed age or at fixed weight by inclusion of the appropriate covariate in the analyses. However, the traits analysed with the two slaughter criteria were quite different, and examination of the change in genetic and phenotypic parameters with change in the slaughter criterion was only possible for a few traits. In the Wolf study, lambs were slaughtered at fixed weight, but no parameters were estimated for slaughter at fixed age. Parameter estimates from the literature are given in Tables 1.2 and 1.3 for lambs slaughtered at fixed age and fixed weight respectively.

Several authors have taken estimates of heritabilities, phenotypic and genetic correlations for production traits from various sources with lambs slaughtered according to age or weight or age and weight. In some cases, the genetic correlation was assumed to equal the phenotypic correlation, heritability estimates from cattle were used or genetic parameters were assumed. The lack of reliable parameter estimates implies that the genetic variance-covariance matrix has a high probability of not being positive definite, especially as the number of traits increases (Hill and

TABLE 1.2

Estimates of phenotypic and genetic parameters for carcass traits of lambs slaughtered at fixed age

Trait	Author	Slaughter weight	Lean weight	Lean prop.	Fat weight	Fat prop.	Backfat depth
Slaughter weight	P	*22*	88	-31	79	49	37
	Be	25					53
Lean weight	P	81	*31*	-3	69	37	33
Lean prop.	P	-14	39	*55*	-62	-71	-30
Fat weight	P	71	30	-74	*25*	91	45
Fat prop.	P	71	-16	-93	88	*36*	39
	G						76
Backfat depth	P	59	35	-26	65	52	* 9*
	Be	50					10
	L						34
	M						23
	O						28

B : Bowman and Hendry, 1972

Be : Bennett, Meyer, Kirton, Smith and Jagusch, 1983

G : Gooden, Beach and Purchas, 1980

Bo : Bodkin, Field, Riley, Nolan and Roehrkasse, 1969

K : Kempster, Avis, Cuthbertson and Harrington, 1976

Ki : Kirton and Johnson, 1979

L : Lax, 1973

M : McEwan, Fennessy, Clarke, Hickey and Knowler, 1984

N : Nicol and Parratt, 1984

O : Olson, Dickerson, Crouse and Glimp, 1976

P : Parratt, Burt, Bennett, Clarke, Kirton and Rae, 1987

W : Wolf, Smith, King and Nicholson, 1981

Heritabilities (x100) on the diagonal, genetic correlations (x100) below the diagonal and phenotypic correlations (x100) above the diagonal



TABLE 1.3

Estimates of phenotypic and genetic parameters for carcass traits of lambs slaughtered at fixed weight

Trait	Author	Slaughter age	Lean weight	Lean prop.	Fat weight	Fat prop.	Backfat depth
Slaughter age	W B	* 7* 28					
Lean weight	W Bo P		*23* 39 45	21		-15	4
Lean prop.	W Bo K		41	*41* 40		-93	-61 -53
Fat weight	Bo Ki N P				*44* 50		53 53 55
Fat prop.	W Bo Ki N		-56	-98		*37* 54	68 47 67
Backfat depth	W B Be M		-47	-80		74	*21* 40 14 28

List of authors as in Table 1.2

Heritabilities (x100) on the diagonal, genetic correlations (x100) below the diagonal and phenotypic correlations (x100) above the diagonal

Thompson, 1978). Such a matrix implies that some heritabilities, genetic correlations or partial genetic correlations have estimates outside their bounds.

The various selection criteria, given the selection objectives, suggested by authors in Table 1.1 could be compared for their efficiency in improving lean meat production, using the genetic and phenotypic parameter estimates from a large data set. The parameters of Parratt et al (1987) were estimated using Henderson Method 3 on data from 1431 lambs representing 110 sire families, but the eigenvalues derived from a canonical transformation of Parratt's phenotypic and genetic variance-covariance matrices were not positive definite. Hill and Thompson (1981) demonstrated that even with 160 half-sib families of 10 progeny per family, the probability of non-positive definite variance-covariance matrices was about 0.50 for 10 traits and essentially 1.00 for at least 14 traits, when the traits were phenotypically and genetically uncorrelated with heritabilities of 0.25. Sales and Hill (1976) examined the effects of inaccurate parameter estimates on selection indices and cautioned against the uncritical use of poorly estimated parameters. Therefore, conclusions about the efficiency of the various selection criteria for improving lean meat production would be of little value if the genetic and phenotypic parameters of Parratt et al (1987) were used. One of the advantages of restricted maximum likelihood methodology (REML; Thompson, 1982) rather than Henderson Method 3 for variance component estimation is that the canonical variance-covariance matrix is positive definite. The REML parameter estimates from the

data of Parratt et al (1987) would be useful for comparing different selection programs.

### Selection objectives and criteria

The main selection objectives examined by various authors were linear combinations of carcass lean and fat weights or carcass lean and fat proportions (Table 1.1). Lean growth rate (LGR) can be defined as the rate of lean meat deposition but several authors have used different definitions. Bennett and Clarke (1984) defined the selection objective of LGR as an index of carcass weight (CWT) and carcass fat proportion adjusted for liveweight (AFP) with the phenotypic regression coefficients of lean weight on CWT and lean weight on AFP for index coefficients, namely  $LGR = 0.51 CWT - 0.14 AFP$ . Purchas, Bennett and Dodd (1985) included the regression of lean weight on carcass fat depth adjusted for weight (AFD) and obtained  $LGR = 0.45 CWT - 0.25 AFD$  as their selection objective. Rae (1984) used New Zealand economic weights for CWT and AFD to define a selection objective of  $0.47 CWT - 0.14 AFD$ , which is remarkably similar to the objectives of Bennett and Clarke (1984) and Purchas et al (1985).

Simm and Dingwall (1985) determined selection criteria for a selection objective of carcass lean and fat weights using a desired gains procedure. The responses to selection were estimated for a range of economic values per unit of carcass lean weight relative to an economic value of -1 per unit of carcass fat weight. An index with relative economic values of 3 and -1 for carcass lean and fat weights, respectively, was chosen as the expected response

in lean weight was approaching its asymptote while the expected increase in fat weight was small. The selection criteria included liveweight at fixed age (LW), ultrasonic muscle (UMD) and fat depths (UFD) and was essentially  $LW + (UMD - UFD)$ . Simm (1986) used New Zealand economic weight for carcass lean and fat weights and obtained the selection index  $LW + 2(UMD - UFD)$ .

Bennett and Clarke (1984) compared indices of an individual's measurements with indices containing information on half-sib measurements and indices with carcass measurements from half-sibs or from progeny, for improvement in lean growth rate, as defined by Bennett and Clarke (1984), and in carcass fat proportion adjusted for liveweight. For both objectives, the marginal gain from using carcass information in both half-sibs and progeny did not merit the use of carcass dissection. A selection index of individual and half-sib liveweights at fixed age with individual and half-sib ultrasonic backfat depths was recommended for both selection objectives. Rae (1984) also suggested that there may be little advantage from progeny testing when ultrasonic information is available on the live animal.

It may be reassuring in that even when each of the authors have used their own set of phenotypic and genetic parameters or have used a different approach to the problem, that the selection objectives are similar as are the selection criteria and the conclusions about the use of progeny testing. Or it may just be fortuitous!

More precise estimates of the genetic and phenotypic parameters are required to determine the optimal selection criteria

for the selection objectives which will most efficiently improve the production of lean meat.

#### Results from selection experiments

A divergent selection experiment, with a control, for ultrasonic backfat depth adjusted for liveweight in Coopworth sheep was started in 1980 (Fennessy, Greer and Bass, 1982). Significant differences in carcass subcutaneous fat depths between crossbred progeny from lean and fat line sires were found (Table 1.4). The fat line had higher carcass fat proportion at 13.5kg carcass weight. After four years of selection in the purebreeds, the difference in ultrasonic backfat depth at constant weight between the fat and lean lines was 2.3mm (a difference greater than the mean of the control line of 2.1mm) (Fennessy and Lord, 1985).

Bennett, Meyer and Kirton (1983) selected Southdown and Suffolk rams on ultrasonic backfat depth adjusted for liveweight. Crossbred progeny were slaughtered at 20 or 30 weeks of age. Progeny from lean Suffolk rams had lower carcass subcutaneous fat depths and less internal fat (Table 1.4). The differences between the progeny of lean and fat Southdown rams for several carcass traits were not consistent with expectation. Identification of lean or fat rams on the basis of ultrasonic backfat measurements may be less accurate in breeds of low mature weight, such as the Southdown, than in larger breeds, like the Suffolk. Therefore, further research is required to evaluate performance testing procedures to enable efficient selection for lean meat production.

TABLE 1.4

Responses to selection on ultrasonic backfat depth  
adjusted for liveweight

	Slaughter weight (kg)	Carcass weight (kg)	Fat + C (mm)	GR (mm)	Fat weight (kg)	Fat%	KKCF ++ (g)
Coopworth \$							
Lean		13.5	1.93	6.16	2.81	20.9	
Fat		13.5	2.31	6.70	2.93	21.6	
Suffolk #							
Lean	39.2	17.0	4.0	12.0			348
Fat	39.1	17.0	4.2	12.5			379
Southdown #							
Lean	34.7	15.3	3.6	12.2			337
Fat	33.9	14.8	4.1	11.4			308

+ Carcass fat measurements

  C : fat depth over the 12th rib, 3.5cm from the midline

  GR : fat depth over the 12th rib, 11cm from the midline

++ Kidney knob and channel fat (internal fat)

\$ Fennessy, Greer and Bass, 1982

# Bennett, Meyer and Kirton, 1983

### Genetic variation in physiological traits

Physiological traits, such as blood metabolites or electrophoretic variants, could be used to improve the prediction of breeding values for carcass traits in the live animal, if the physiological trait was genetically correlated with the breeding value. However, if the genetic parameters are inaccurate, then the extra response from using the physiological trait in the selection criteria will usually be over-estimated. If the physiological trait is actually uncorrelated, but is assumed to be correlated, with the selection objective, then the loss in efficiency from its inclusion in the selection criteria is equal to the predicted benefit (Sales and Hill, 1976).

There has been some interesting research on the phenotypic relationship between physiological traits with carcass traits. Since insulin stimulates fat deposition, Munro, Geenty and Bickerstaffe (1984) estimated the phenotypic relationship between plasma insulin and blood glucose with carcass fat, but found that the correlations were dependent on age at weaning and sampling. Fennessy and Lord (1985) measured the in vitro tritiated thymidine incorporation into skeletal muscle of progeny from rams selected for high or low ultrasonic backfat depth. Muscle tissue from high line progeny generally incorporated more tritiated thymidine than low line progeny, but the sign and magnitude of the differences were age dependent. The intramuscular fat of lean lambs contained more triglyceride and the fatty acids were less saturated than in fatter lambs, but the lean and fat lambs were from different sources (Siebert, 1984).

Research on differences in physiological traits between genetically lean and fat lambs will be of great benefit to the understanding of the biochemistry of lipogenesis and lipolysis, protein synthesis and degradation. However, the use of physiological traits in selection programmes should wait until more precise genetic and phenotypic information is available.

### Summary

In conclusion, the results from the selection experiments are encouraging in that lean meat production can be effectively improved through selection programmes. However, it is also apparent that the optimal selection objective and corresponding selection criterion for a given production system can only be determined when precise estimates of the genetic and phenotypic parameters of lean meat production are available. The establishment of selection lines for particular traits will be valuable for the assessment of new selection criteria, in particular methods of estimation of carcass composition on the live animal, and also may provide a useful tool for research on the physiology of lean meat production in sheep.



## CHAPTER 2

### COMPARISON OF TERMINAL SIRE BREEDS FOR GROWTH AND CARCASS TRAITS IN CROSSBRED LAMBS

#### INTRODUCTION

Information on growth and carcass traits of progeny from different terminal sire breeds is required by producers of commercial lambs to facilitate choices in relation to production system and changes in market requirements. Previous work by the Animal Breeding Research Organisation (ABRO) (Wolf, Smith and Sales, 1980) and the Meat and Livestock Commission (MLC) (Croston, Guy, Jones and Kempster, 1983) compared several terminal sire breeds. This study extended the range of breeds to include two recent imports from France (Charollais and Charmoise) and a synthetic breed (Meatline; Fell, 1979). The other breeds compared were the Texel which has been noted previously for an unusually high lean proportion, the Oxford which is the largest Down breed and the Texel-Oxford cross. The Texel-Oxford line was derived at ABRO from three to four generations of interbreeding of a Texel-Oxford cross.

#### MATERIALS AND METHODS

##### Ewe flock

Crossbred ewe lambs were produced, from 1979 to 1981, on an Ayrshire hill farm, out of Scottish Blackface ewes mated to rams of several crossing sire breeds (Scottish Blackface, Border Leicester, Oldenburg, Texel, East Friesian, Cambridge, ABRO Damline and

Romney). After weaning, the crossbred ewe lambs were transferred to ABRO's lowland experimental farm in Staffordshire.

### Terminal sires

The crossbred ewes were mated at 6 months of age and for 2 subsequent years to Texel, Texel-Oxford, Charollais, Charmoise and Meatline ram lambs. Oxford rams were also used in 1981. The Texel rams were the progeny of imported Dutch and French stock. In each year, there were three or four rams of each breed, although in 1979 and 1980, nine Texel-Oxford rams were used, making a total 62 rams used during the experiment. Different rams were used each year and were chosen as being representative of the breeds.

Crossbred ewes within each age group and crossbred type were randomly allocated each year to each sire breed, resulting in an average of 19 crossbred ewes per ram, with single-sire paddock matings. Immediately after lambing, mis-mothering was prevented by individually penning ewes and their litters for 12 h, and there was no fostering. Any lamb born outside the range of  $145 \pm 4$  days of its dam's recorded mating date was considered of uncertain pedigree and not included in the analysis.

Records kept for each lamb born were breed of sire and maternal grand sire, identity of sire and dam, date of birth, sex and birth-rearing type. The lambs were weighed at birth and at 4, 8, 12 and 16 weeks of age ( $\pm 3$  days). Weaning took place when lambs were 16 weeks old.

### Lamb slaughter groups

Fixed age. Each year, 50 pairs of twin-reared lambs, from

2- or 3-year-old ewes and representing the six terminal sire breeds, were randomly selected for slaughter and dissection at either 4.5 months of age ( $\pm 7$  days) or 5.5 months of age with mean live weights of about 35 and 40kg respectively.

Fixed weight. Half the remaining lambs (with odd-number identities) were slaughtered when reaching a fixed weight of 36 kg for ewe lambs and 38 kg for castrates.

Fat cover. The third group of lambs (with even-number identities) were slaughtered at equal estimated level of fat cover. The level of fat cover was assessed by the condition scoring technique. All carcasses were graded by the MLC. In addition, carcass appraisal data were available for lambs slaughtered at fixed weight or level of fat cover.

#### Carcass dissection

Carcass dissections were carried out, each year, on the 50 pairs of twin-reared lambs slaughtered at fixed ages. The lambs were all slaughtered at one abattoir and MLC carcass classification information (MLC, 1981) and cold carcass weights were recorded for all lambs before being sent for dissection. Half the lambs were dissected by the MLC, Blisworth, and half by the East of Scotland College of Agriculture (ESCA) with the six terminal sire breeds represented equally at both locations. The kidney knob and channel fat (KKCF) was removed and the carcass was cut into eight standard joints using anatomical reference points (Cuthbertson, Harrington and Smith, 1972). Each joint was dissected into lean, subcutaneous fat, intermuscular fat, bone and waste. Information regarding the

differences in time and place was available from both within and between twin pairs (litters). The intra-litter correlation coefficient was calculated and the within- and between-litter estimates were weighted accordingly to give an overall estimate of the differences between the two dissection centres and times of slaughter. For slaughter and carcass traits the intra-litter correlation coefficient ranged from 0.21 to 0.26.

### Statistical analysis

Hierarchical least-squares analysis of variance was performed for each trait with progeny nested within dams, which were nested within sires (Harvey, 1960). Effects were fitted for terminal sire breed, breed of maternal grand sire, day and year of birth of lamb, age of dam at lambing, birth type and sex of lamb and all two-way interactions, with effects being tested against the appropriate error mean squares. In the birth weight model, a birth type effect was included. However, as the rearing type of a lamb was not always equal to its birth type, due to mortality of its sibs, a birth-rearing type effect was included in the model for postnatal traits. Birth-rearing categories were (1,1), (2,1), (2,2), (3,1), (3,2) and (3,3) where the first digit refers to birth type and the second to rearing type. Date of birth was included in the analysis of birth weight and carcass traits, as the lambs were slaughtered on fixed dates. Initially, all terms were included in the models. Effects were, then dropped sequentially using the backward elimination technique (Hocking, 1976) until only significant ( $P < 0.10$ ) effects remained. The least-squares constants

presented were obtained from the resulting reduced model for each trait. For each comparison of breed constants, the appropriate standard error of the difference was calculated, due to the unbalanced nature of the data, and a t test performed.

## RESULTS

There was no statistically significant differences in litter size from birth to 16 weeks between the terminal sire breeds. Although at 16 weeks, the litter size of crossbred ewes mated to Oxford rams was 1.54 compared with the average of the other breeds of 1.72 (s.e. 0.12). It is necessary that there should be no confounding of litter size and sire breed, when the performance of progeny from terminal sire breeds is compared, and therefore, birth-rearing type was included in the model.

### Live weights

The least-squares constants for lamb live weight and rates of weight gain at the various ages are given in Table 2.1. By 12 and 16 weeks of age, the progeny from Oxford and Texel-Oxford rams were heaviest, those from Charmoise the lightest, while the Charollais, Meatline and Texel progeny had intermediate weights.

Daily growth rates dropped steadily with age, until 12 weeks when the mean rate decreased from 261 to 150g/day at 16 weeks. The ranking of the sire breeds for rate of weight gain in each of the 4-weekly periods from birth to 16 weeks followed no consistent pattern, although differences between breeds were evident after 4 weeks of age. However, from birth to 16 weeks, the Charmoise crosses generally grew slower than the others, while the Texel-

TABLE 2.1

Overall means and least-squares constants for pre-weaning growth traits by sire breed

No.	Birth weight (kg)	Live weight at week				Weight gain between weeks (g/day)				
		4	8	12	16	0 to 4	4 to 8	8 to 12	12 to 16	0 to 16
Overall mean	3.85	12.9	21.4	28.7	32.7	318	300	261	150	257
Sire breed <sup>†</sup>										
Charmoise	258	-0.24a	-1.7a	-1.5a	-1.7a	-23a	-25a	3ab	-8a	-13a
Texel	358	-0.07b	0.1b	-0.3b	-0.3b	7b	-12b	-8a	0ab	-2b
Meatline	263	0.00b	0.1b	-0.4b	0.0b	5b	-4bc	-5a	10b	0bc
Charollais	271	-0.01b	0.1b	0.0bc	0.2b	1b	13cd	-5a	0ab	1bc
Texel-Oxford	659	0.05b	0.5b	0.4c	0.6bc	10b	5cd	-1ab	4ab	4cd
Oxford	119	0.13b	0.9b	1.8d	1.2c	-1b	23e	17b	-6ab	10d
Approx. s.e.	0.04	0.12	0.17	0.18	0.20	3	4	4	4	4

<sup>†</sup> Column values not followed by a common letter differ significantly (P < 0.05)

Oxford and Oxford crosses grew faster.

The ranking of the sire breeds for mean daily weight gain from birth to 16 weeks was the same as for 16-week weight, confirming the close relationship between growth rate and live weight. The ranking of the breeds for mean growth rate and mature live weight was similar ( $r = 0.92$ ; s.e. 0.45), but the Texel crosses had a lower mean growth rate than expected. The estimates of mature weight were obtained from the MLC (1981) and D. Croston (personal communication).

#### Slaughter at fixed live weight

The slaughter ages and weights are given in Table 2.2. At fixed slaughter weight, the lower age of Oxford crosses indicates that they maintained their growth advantage over the other crosses after weaning. Likewise, the Charmoise crosses had later slaughter dates indicating a slower post-weaning growth rate. The Charollais, Meatline and Texel-Oxford crosses reached slaughter weight about 11 days earlier than the Charmoise crosses and 7 days later than the Oxford crosses, although the latter result was not statistically significant. The initial experimental design provided for ewe and castrated lamb slaughter weights of 36 and 38kg respectively, but in practice the range of weights was from 30 to 50kg. In the analysis, the range was restricted to 34 to 40kg in order to obtain more precise estimates of breed differences with slaughter at fixed weight. The slaughter weights for ewe and castrated lambs in the restricted data set averaged 36.9 and 38.2kg respectively. There were no differences in carcass weight among

TABLE 2.2

Overall means and least-squares constants for slaughter traits by sire breed

	Lambs slaughtered according to									
	Fixed weight					Level of fat cover				
	No.	Age (days)	Carcass weight (kg)	Carcass conformation (MLC)	Subcutaneous fat cover (MLC)	Slaughter age (days)	Slaughter weight (kg)	Carcass weight (kg)		
Overall mean	651	154	16.7	8.4 <sup>+</sup>	8.0 <sup>++</sup>	993	145	37.5	16.5	
Sire breed <sup>+++</sup>										
Charmoise	104	10a	-0.1a	0.7	0.9	128	2a	-2.2a	-0.8a	
Texel	125	2ab	0.0a	-0.3	-0.6	188	1a	0.4b	0.2bc	
Meatline	93	0b	-0.1a	-0.5	-0.3	131	0a	-0.1b	-0.1b	
Charollais	93	-1b	0.1a	0.6	0.2	133	2a	-0.6ab	-0.1b	
Texel-Oxford	196	-3b	0.0a	-0.4	-0.4	347	0a	0.8b	0.1bc	
Oxford	40	-9b	0.0a	-0.1	0.2	66	-5a	1.7b	0.7c	
Approx. s.e.		3	0.17				2	0.31	0.14	

+ Conformation: 1 = poor; 15 = good

++ Subcutaneous (external) fat cover overall: 1 = extremely little fat; 15 = extremely fat

+++ Column values not followed by a common letter differ significantly ( $P < 0.05$ )



the sire breeds. The MLC overall carcass conformation scores for Charmoise and Charollais crosses were one point higher than those for the other breeds. The overall subcutaneous fat cover scores for the Charmoise and Texel crosses were the highest and lowest respectively. The MLC carcass appraisal scheme also records conformation scores for the leg, loin and shoulder joints separately and the residual correlation coefficients between overall conformation scores and these individual joint scores were 0.88, 0.89 and 0.91 (s.e. 0.04) respectively.

#### Slaughter at constant level of fat cover

For lambs slaughtered according to level of fat cover, there were no statistically significant differences in slaughter age, although the Oxford crosses were slaughtered about 6 days earlier than the other crosses and at heavier slaughter weights. The Charmoise crosses had significantly lighter slaughter weights than the other crosses. The ranking of the sire breeds for carcass weight was the same as for slaughter weight with the Oxford and Charmoise crosses having significantly heavier and lighter weights, respectively, than the other crosses. For each breed, the MLC overall carcass conformation scores and subcutaneous fat cover scores were similar for lambs slaughtered according to fixed weight or level of fat cover. The MLC recommend that producers market the majority of lambs with MLC carcass classifications of fat class 2 or 3L and 76% of the lambs slaughtered according to fat cover were in these fat classes.

### Carcass dissection

The results are given in Table 2.3. Breed differences in slaughter weight were similar when lambs were slaughtered at different ages (140 and 170 days) to those when lambs were slaughtered according to body condition at an average of 145 days of age. This suggests that the relative differences between breeds were constant over time and the lack of a statistically significant sire-breed x slaughter time interaction is consistent with this.

Carcass weights of Charollais and Texel Oxford crosses were significantly heavier than the Charmoise crosses by 1.2kg, and the other breed crosses were 0.8kg heavier but not significantly. The Charmoise crosses had significantly higher killing-out proportions than the Texel, Oxford and Texel-Oxford crosses, with the Charollais and Meatline crosses intermediate.

The carcasses of Charmoise crosses had a lower total lean weight than the others by 1.2kg, on average, and Texel-cross carcasses had lower total fat weight by 1.0kg, on average. The ranking of the breeds for lean weight was opposite to the ranking for fat weight. Similarly, the proportions of carcass lean and fat had the same rankings as for total lean and fat weight, respectively, although the breed differences were larger. The Texel crosses had proportionately more lean, 62g/kg carcass weight, and less fat, 73g/kg, than the Charmoise crosses, with the Meatline and Charollais crosses intermediate. The Texel crosses had proportionately more lean, 50g/kg, and less fat, 47g/kg than the Oxford crosses, while the Texel-Oxford crosses had proportionately more lean, 21g/kg, and less fat, 19g/kg, than the Oxford and were

TABLE 2.3

Overall means and least-squares constants for carcass traits by sire breed

	No.	Slaughter	Carcass	Killing	Half-carcass weight		Composition of carcass			
		weight (kg)	weight (kg)	out (g/kg)	Lean (kg)	Fat (kg)	Lean (g/kg carcass weight)	Fat Bone		
Overall mean	293	40.8	16.8	413	4.6	2.3	1.3	553	276	159
Sire breed <sup>+</sup>										
Charmoise	50	-2.8a	-0.8a	12a	-0.5a	0.2a	-0.1a	-27a	35a	-10a
Texel	52	-0.6b	-0.2ab	-2b	0.2b	-0.4b	0.0b	35b	-38b	2bc
Meatlinec	48	0.2b	-0.1ab	-1ab	0.0b	0.0a	0.0bc	-1c	0cd	2bc
Charollaise	47	0.5b	0.5b	6ab	0.1b	0.1a	0.0bc	1c	4cd	-5ab
Texel-Oxford	77	1.2b	0.4b	-4b	0.2b	0.0a	0.1c	6c	-10d	3c
Oxford	19	1.6b	0.3ab	-11b	-0.1ab	0.1a	0.1bc	-15ac	9ac	8c
Approx. s.e.		0.50	0.26	3.3	0.07	0.06	0.02	4.0	4.6	1.7
Slaughter time										
4.5 months	149	-2.7	-0.8	0	-0.2	-0.2	0.0	6	-10	4
s.e.		0.22	0.20	2.5	0.03	0.03	0.01	1.7	2.0	0.7
Dissection centre										
ESCA	151		-0.4	-7	-0.3	0.1	0.0	-27	28	4
s.e			0.11	1.5	0.03	0.03	0.01	1.7	1.8	0.7

<sup>+</sup> Column values not followed by a common letter differ significantly (P<0.05)

similar to the mean of the Texel and Oxford breed crosses. The residual correlation of total lean weight with total fat weight was 0.45 (s.e. 0.06) and that of carcass lean proportion with fat proportion was -0.90 (s.e. 0.06), after fitting fixed effects.

Mean slaughter weights at 4.5 and 5.5 months of age were 38.1kg and 43.5kg respectively. Carcasses of the later slaughter time were 1.6kg heavier and contained proportionately less lean, 12g/kg carcass weight, more fat, 20g/kg and less bone, 8g/kg. The killing-out proportions at the two slaughter times were the same. The sire-breed x slaughter-time interaction was not statistically significant for any trait.

Differences between dissection centres were statistically significant for all carcass traits except total bone weight. The ESCA carcasses were, on average, 0.8kg lighter than the MLC carcasses. This resulted in a difference in killing-out proportion of 14g/kg. ESCA carcass total lean and fat weights were 0.66kg lighter and 0.26kg heavier, respectively, than MLC weights. Thus the ESCA lean proportion was lower, 54g/kg carcass weight, and the fat proportion was higher, 56g/kg.

The proportions of total carcass lean found in each of the eight joints are given in Table 2.4. There were statistically significant differences between sire breeds for all joints except chump and middle neck. However the maximum difference between breeds was 16g/kg carcass lean for the leg joint. This would result in a maximum difference between breeds of 40g lean weight for the leg joint, which is unlikely to be economically significant. Sire-breed differences of higher priced joints (leg, chump, loin and

TABLE 2.4

Proportion of carcass lean (g/kg carcass lean) in the different joints by sire breed

	No.	Leg	Chump	Loin	Breast	Best-end neck	Middle neck	Shoulder	Scrag
Overall mean	293	255	83	100	114	77	120	216	30
Sire breed <sup>+</sup>									
Charmoise	50	-8a	0a	3a	6a	2a	0a	-4a	0ab
Texel	52	8c	-1a	-4b	-4b	-5b	2a	4b	1ab
Meatline	48	3bc	1a	1ab	-1b	1a	-2a	-2ac	-2b
Charollais	47	0ab	-1a	2a	1ab	1a	-2a	1ab	0ab
Texel-Oxford	77	1b	1a	-4b	0b	-2b	2a	1bc	1a
Oxford	19	-4ab	0a	3ab	-2b	3a	1a	0abc	-1ab
Approx. s.e.		1.6	0.9	1.4	1.3	0.9	1.0	1.1	0.8
Slaughter time									
4.5 months	149	4.0	-0.7	-1.7	-2.3	-0.3	-0.7	0.6	1.7
s.e.		1.2	0.4	0.6	0.6	0.4	0.6	0.5	0.6
Dissection centre									
ESCA	151	-0.6	3.3	-5.0	3.7	-1.8	2.3	-0.4	1.8
s.e.		0.7	0.6	0.6	0.9	0.4	0.5	0.5	0.6

<sup>+</sup> Column values not followed by a common letter differ significantly (P<0.05)

best end neck) were also small (9g/kg). These results show small but statistically significant differences in the lean tissue distribution, of crossbred lambs, due to sire breed, a finding also noted by Wolf (1982). As with carcass traits, there were small differences between slaughter times and between dissection centres for each joint. There were statistically significant year x dissection-centre interactions for all joints except leg, loin and middle neck.

### DISCUSSION

For all the traits analysed, there was no evidence of a crossing-sire-breed (sire of ewe) x terminal-sire-breed interaction. This result agrees with that of Wolf et al (1980) and suggests that, within the range of crossbred ewe types considered in the experiments, the crossbred ewe type is of little importance when comparing the performance of progeny from various terminal sire breeds.

As slaughter weight largely determines fat content of the carcass, Bradford (1974) suggested a slaughter weight for crossbred lambs of 0.60 to 0.65 of the mean mature weight of their parental breeds as a commercial guide to standardise carcass composition. However, the proportion of assessed carcass subcutaneous fat is a common alternative slaughter criterion in the current United Kingdom market. Accordingly, the data were adjusted to an equal proportion of dissected subcutaneous fat in the carcass using the pooled within-breed regression, there being no evidence of statistically different regression coefficients for the six breeds. The results

from this analysis were then combined with those of two other trials (Table 2.5), using the overlap in breeds among trials, to give information on a total of 15 terminal sire breeds. The least-squares estimates of breeds were obtained from a weighted analysis of variance using the number of observations for each of the breeds means as weights and fitting constants for each trial, in an attempt to minimize the problems created by combining data from different environments and different years.

At the same proportion of carcass subcutaneous fat, slaughter age and carcass weight were positively correlated between sire breeds ( $r = 0.81$ ,  $P < 0.05$ ) which suggests that breeds of heavier mature weight tend to take longer to reach a particular level of subcutaneous fat, which results in heavier carcasses. This is in agreement with the hypothesis of McClelland and Russel (1972) that if breeds of different mature weight were slaughtered at the same degree of maturity, then the fat proportion would be similar for all breeds. At the same proportion of carcass subcutaneous fat the correlation coefficients of estimated breed mature weight with slaughter age and carcass weight were 0.72 and 0.84 ( $P < 0.05$ ), respectively. This indicates that the growth rates of crosses from the 15 breeds studied, tend to follow a well-established pattern, where weight for age rankings are reasonably consistent from birth, through weaning, to slaughter.

From these results it may be concluded that a first approximation to the performance of a terminal sire breed may be obtained from a knowledge of its mature weight. Growth rates, slaughter age and weight for a similar level of fat cover could be

TABLE 2.5

Comparative performance of crossbred lambs from 15 terminal sire breeds at the same proportion of carcass subcutaneous fat (pooled results from three trials)

Sire breed	Trial <sup>+</sup>	Mature weight (kg) <sup>++</sup>	Carcass weight (kg)	Slaughter age (days)
Southdown	3	61	14.0	131
Charmoise	1	62\$	15.8	164
Dorset Down	2,3	77	15.3	144
Hampshire Down	3	78	15.4	145
Ile de France	2,3	78	16.2	158
Oldenburg	2	79\$	16.3	170
North Country				
Cheviot	3	82	16.6	170
Charollais	1	85\$	17.5	162
Meatline	1	85\$	17.6	167
Texel	1,2,3	87	17.3	169
Suffolk	2,3	91	17.0	156
Texel-Oxford	1	93	17.7	165
Border Leicester	3	94	17.5	191
Oxford	1,2,3	100	17.2	160
Wensleydale	3	113\$	18.3	207

<sup>+</sup> 1 = Current trial; 2 = Wolf, Smith and Sales (1980),  
3 = Croston, Guy, Jones and Kempster (1983)

<sup>++</sup> Mature weights from MLC (1981) except those marked \$ from D. Croston, MLC (personal communication).



then estimated. Deviations from these first approximations are expected, such as the Texel in proportions of carcass lean and fat.

Different terminal sire breeds may be suited to different production systems. For example, when the objective is to produce lamb carcasses to a fixed level of fat cover, the larger sire breeds (e.g. Suffolk and Texel-Oxford) would be expected to produce heavier and older lambs than those of the lighter sire breeds (e.g. Southdown and Charmoise). Changes in the production system could be met by changing the terminal sire breed in accordance with their mature weight.

Market requirements for carcass quality and perhaps breed acceptance may also affect the choice of terminal sire breed. For example, substitution of the Suffolk by the Texel may not be economically viable unless the disadvantage of greater slaughter age, due to lower growth rate, is offset by a premium for the production of lean carcasses. Other problems associated with changes in live weight such as lambing difficulties and subsequent mortality, will also have to be considered. However, the currently important traits of growth rate, carcass weight and level of fat cover can readily be determined by choosing among breeds of terminal sires, on the basis of their mature live weight.

## SUMMARY

Performance records for the progeny of matings of Oxford, Texel, Texel-Oxford, Charollais, Charmoise and Meatline rams with crossbred ewes were analysed. The lambs, born from 1980 to 1982, were randomly allocated to three slaughter groups: (1) slaughter at fixed weights of 36 and 38kg for ewe and castrated lambs; (2) slaughter according to estimated fat cover; (3) slaughter at a fixed age of 4.5 or 5.5 months with half-carcass dissection. The analyses were by least squares and effects were fitted for terminal sire breed, breed of maternal grand sire, year of birth, age of dam at lambing, birth-rearing type and sex of lamb and all two-way interactions. The results followed a well-established pattern where weight for age rankings were constant from birth, through weaning, to slaughter. Progeny of Oxford rams were the heaviest, followed by Texel-Oxford, Meatline and Charollais, Texel and Charmoise in that order. Lambs sired by rams of low mature weight reached a fixed weight at a later age than those sired by rams of high mature weight. They also reached a similar degree of fat cover at an earlier age and at lighter weights than the larger breeds. The carcass traits indicated that Texel crosses had a higher lean and lower fat proportion than would be expected from their growth and mature weight.

The comparative performance of crossbred lambs from 15 terminal sire breeds was assessed, at the same proportion of carcass subcutaneous fat, by combining the results of three experiments.

## CHAPTER 3

### RESPONSES IN LAMB PERFORMANCE FROM SELECTION ON SIRE 100-DAY WEIGHT

#### INTRODUCTION

The main current selection objective in terminal sire breeds of sheep in the United Kingdom is lamb growth rate (Meat and Livestock Commission (MLC), 1983). However, genetic improvement of growth rate in lambs is difficult due to its low heritability with natural rearing (Wolf, Smith, King and Nicholson, 1981). Adult size tends to be more heritable than juvenile size, but Croston, Read, Jones, Steane and Smith (1983) found that selection on 18-month weight was not very effective in the improvement of lamb growth. Owen, Brook, Read, Steane and Hill (1978) selected on ram 90-day weight, with artificial rearing, to remove post-natal maternal effects, and concluded that this was an effective method of selecting rams for improving lamb growth rate. This study estimated the correlated responses in the performance of naturally-reared lambs from crossbred ewes due to selection on ram 100-day weight with artificial rearing.

#### MATERIAL AND METHODS

Between 1978 and 1982, 174 Texel and Texel-Oxford rams were artificially reared and selected on live weight at 100 days of age. The Texel-Oxford line was derived at the Animal Breeding Research Organisation (ABRO) from three to four generations of interbreeding

of a Texel-Oxford cross. The rams were born and artificially reared on ABRO's experimental farm at Blythbank, Tweeddale. They received their dam's colostrum and were removed from the dam within 6h of birth. After 12 to 18h, the rams were fed half-strength, warm substitute milk, to accustom them to an artificial teat. The milk was gradually increased to full strength, ad libitum, over 2 to 3 days. To enable weaning at 6 weeks of age, with a minimum of 10kg live weight, the rams were also given pellets of whole barley and fish meal supplement twice daily at 4 weeks of age and once daily at 5 weeks of age. After weaning, the rams were individually penned and fed ad libitum until the end of test at 16 weeks of age. At the end of test, the lambs were turned out to grass and the pelleted food was reduced as they became accustomed to the grass. The rams were run with, or grazed alongside, ewes to help develop normal mating behaviour.

Each year, groups of rams were selected for high and low 100-day weight, adjusted for birth type (single or twin born), age of dam, date of birth and age of ram at weighing. For selection purposes, the adjustment factors were calculated from the rams born in each year. Thus, there were different factors in different years. To determine comparable selection differentials for each year, common adjustment factors were used for all rams, using the combined data on 174 rams. Breed-of-ram and year-of-birth effects were also included in the analysis. Five lambs with a disease history or with little growth over a 3-week period were discarded from the selection and the analysis.

The rams were mated at 6 months of age to a flock of

crossbred ewes on ABRO's lowland experimental farm in Staffordshire. The flock consisted of crosses out of Scottish Blackface ewes by rams of eight breeds (Scottish Blackface, Border Leicester, Oldenburg, Texel, East Friesian, Cambridge, ABRO Damline and Romney). Ewes within each age group and crossbred type were randomly allocated each year to the rams, resulting in an average of 19 crossbred ewes per ram, with single-sire matings. Mismothering was prevented by individually penning ewes and their litters immediately after lambing, and there was no fostering. The crossbred lambs were reared naturally under normal management practice. Any lamb born outside the range of  $145 \pm 4$  days of its dam's recorded mating date was considered of uncertain pedigree and not included in the analysis. Records kept for each lamb born were breed of sire and maternal grand sire, identity of sire and dam, date of birth, sex and birth-rearing type. The lambs were weighed at birth, 4, 8, 12 and 16 weeks of age ( $\pm 3$  days) and were weaned at 16 weeks of age.

Each year, half of the lambs (with odd-number identities) were slaughtered at a fixed weight of 38kg for ewe lambs and 40kg for castrated male lambs. The remaining lambs were slaughtered at an equal estimated level of fat cover. The level of fat cover was assessed by the farm staff using the condition-scoring technique of the MLC (1981). The lambs were all slaughtered at one abattoir, where MLC carcass classification (MLC, 1981), appraisal information and cold carcass weight were recorded.

Hierarchical least-squares analysis of variance was performed for each trait with progeny nested within dams, which were

nested within sires. Effects were fitted for terminal sire breed, breed of maternal grand sire, day and year of birth of lamb, age of dam at lambing and sex of lamb and all two-way interactions, with effects being tested against the appropriate mean square. For the birth-weight model, a birth-type effect was included. However, as the rearing type of a lamb was not always equal to its birth type, due to mortality of its sibs, a birth-rearing type effect was included in the model for post-natal traits. For lambs slaughtered at fixed weight, actual slaughter weight was included in the model as a covariate. Initially, all terms were included in the models. Effects were then dropped sequentially using backward elimination (Hocking, 1976) until only significant ( $P < 0.10$ ) effects and interactions remained.

When selection is on trait 1 (sire 100-day weight) for improvement in trait 2 (lamb trait), one of the parameters required for predicting the genetic response through indirect selection can be estimated, namely the co-heritability ( $r_A h_1 h_2$ ) (Yamada, 1968), where  $h^2_i$  is the heritability of trait  $i$  and  $r_A$  is the genetic correlation between the two traits. The co-heritability can be estimated from the offspring-parent regression and, analogous to the realized heritability, from the ratio of the response in the progeny to the selection differential of the parents (Falconer, 1981), with response defined as the difference in mean phenotypic value of progeny from high- and low-weight sires for trait 2. The most efficient design for estimating co-heritability is offspring-parent regression with selection of high and low groups of parents. However, the difference in efficiency between the two methods from a

single generation of selection is small if the co-heritability is low (Hill, 1971). Both methods were used and the results compared.

## RESULTS

The numbers of rams and progeny in the high and low selection groups by year and breed are given in Table 3.1. The selection differentials achieved each year were reasonably similar (Table 3.1), except for the small differential in 1981, when another trial has priority in selection. The difference in adjusted 100-day weight between selected high and low rams, weighted by the number of progeny per ram, was 7.50kg, corresponding to 1.70 standard deviation (s.d.) units.

Differences in weight between the progeny of the high and low rams were generally positive but quite small (Table 3.2). The co-heritability estimates, with standard errors from the offspring-parent regression method, were also low and not significantly different from zero. These co-heritability estimates were, on average, proportionally smaller than the estimates from the realized responses, and the standard errors were of similar magnitude. As the rams were artificially reared and their progeny naturally reared, all the estimates are co-heritability estimates rather than heritability estimates.

The results for lamb slaughter and carcass traits, for the two slaughter criteria are given in Table 3.3. For lambs slaughtered at a fixed weight, the mean slaughter weights were 37.8kg for ewe lambs and 39.7kg for castrated male lambs, close to the weights intended in the design of the experiment. The

TABLE 3.1

Numbers and breeds of rams by year and selection type

Ram year of birth	Ram breed	No. tested	No. selected		Mean+ 100-day weight (kg)	Selection differential (kg)	No. of progeny	
			High	Low			High	Low
1978	Texel	21	4	4	30.5	6.4	108	122
1979	Texel	16	2	2	36.2	10.0	55	57
	Texel-Oxford	36	5	5	36.9	10.2	131	138
1980	Texel	22	2	2	28.9	8.8	44	25
1981	Texel-Oxford	42	3	1	42.5	2.1	78	25
1982	Texel-Oxford	37	5	6	43.1	6.8	143	132
	Overall	174	21	20	35.5	7.5	599	499

+ Overall mean plus least-squares constants, adjusted for birth type and dam age.



TABLE 3.2

Overall means for lamb weight at different ages, the difference between progeny of high and low sires, the offspring-parent regression coefficients and the co-heritability estimates

Age (weeks)	Mean weight (kg)	Residual s.d. (kg)	Response high-low (kg)	Co-		Regression on		Co-		
				s.e.	heritability+	sire weight (kg/kg)	s.e.	heritability++	s.e.	
Birth	4.0	0.65	0.07	0.04	0.05	0.072	0.01	0.005	0.08	0.075
4	12.6	1.88	0.11	0.12	0.07	0.076	0.01	0.015	0.05	0.071
8	20.5	2.83	-0.11	0.18	-0.04	0.076	-0.00	0.023	-0.01	0.072
12	27.5	3.51	0.28	0.23	0.09	0.076	0.03	0.034	0.08	0.087
16	32.5	3.92	0.26	0.26	0.08	0.078	0.03	0.038	0.08	0.086

42.

+ Derived from response/selection differential.  $\text{Response}_2 = 0.5 (r_A h_1 h_2)$  selection differential,  $(\sigma_2/\sigma_1)$  where subscripts denote traits: 1 = sire 100-day weight with artificial rearing; 2 = lamb trait with natural rearing;  $\sigma_1$  = phenotypic standard deviation of trait i.

++ Derived by setting offspring-parent regression coefficients = 0.5  $(r_A h_1 h_2)$   $(\sigma_2/\sigma_1)$

TABLE 3.3

Overall means for progeny slaughter traits with slaughter at fixed weight or level of fat cover, the difference between progeny of high and low sires and the offspring-parent regression coefficients

Trait	Slaughter at fixed weight (no. of lambs = 542)				Slaughter on level of fat cover (no. of lambs = 561)						
	Mean	Residual s.d.	Response high-low	s.e.	Regression on sire weight	Mean	Residual s.d.	Response high-low	s.e.	Regression on sire weight	s.e.
Slaughter age (days)	155	26.6	-3.79	2.65	-0.38	142	29.7	4.17	2.77	0.11	0.418
Slaughter weight (kg)	38.7	2.08				37.2	3.26	0.58	0.30	0.04	0.080
Carcass weight (kg)	17.1	1.55	-0.19	0.15	-0.03	16.6	2.20	0.35	0.20	0.02	0.042
Killing-out proportion (g/kg)	441	40.7	-4.7	3.9	-0.81	445	43.9	2.9	4.1	0.05	0.61
Subcutaneous fat score <sup>+</sup>	7.9	1.71	-0.40	0.16	-0.03	7.5	2.04	-0.14	0.19	-0.01	0.038
Internal fat score <sup>++</sup>	2.3	0.93	-0.24	0.09	-0.02	2.2	0.95	-0.10	0.09	-0.01	0.011
Conformation score <sup>§</sup>	8.0	2.27	-0.34	0.17	-0.03	7.5	1.92	0.17	0.19	0.01	0.27

+ Subcutaneous fat score : 1 (low) to 15 (high)

++ Internal fat score : 1 (low) to 5 (high)

§ Conformation score : 1 (poor) to 15 (good)

coefficient of variation for slaughter weight was lower for lambs slaughtered at a fixed weight (0.054) than for lambs slaughtered according to fat cover (0.088). The progeny from high 100-day weight rams were slaughtered earlier with lighter and leaner carcasses, which had significantly lower subcutaneous fat and internal fat scores and poorer conformation scores than lambs from low-weight rams. For lambs slaughtered at a common condition score, none of the differences between progeny groups were significantly different from zero, but progeny from high 100-day weight rams were slaughtered later and at heavier weights, and the carcass weight and killing-out proportion were also greater. The MLC recommend that producers market the majority of lambs with MLC carcass classifications of fat class 2 or 3L, and the proportion of lambs slaughtered according to fat cover in these fat classes was 0.64.

For the two slaughter criteria, the co-heritabilities for slaughter and carcass traits were generally small and not significantly different from zero (Table 3.4).

#### DISCUSSION

The co-heritability estimates, although not significantly different from zero, suggest consistent trends in crossbred lamb performance from selection on ram 100-day weight with artificial rearing. The results from the two slaughter groups are different, as expected, showing the importance of defining the response criteria when estimating genetic parameters. Progeny of high 100-day weight rams were slaughtered earlier with lighter and leaner

TABLE 3.4

Estimates of co-heritability from offspring-parent regression with slaughter at fixed weight or level of fat cover

	Slaughter at fixed weight	Slaughter on level of fat cover
	Co- heritability <sup>+</sup>	Co- heritability <sup>+</sup>
	s.e.	s.e.
Slaughter age (days)	-0.12	0.03
Slaughter weight (kg)		0.19
Carcass weight (kg)	-0.17	0.10
Killing-out proportion (g/kg)	-0.17	0.01
Subcutaneous fat score	-0.14	-0.06
Internal fat score	-0.23	-0.14
Conformation score	-0.15	0.06
		0.13
		0.34
		0.21
		0.13
		0.20
		0.11
		0.13

+ Co-heritabilities derived from offspring-parent regression estimates.

carcasses when slaughtered at a fixed weight, but were slaughtered later with heavier slaughter and carcass weights when slaughtered according to fat cover. Though the practical value of the co-heritability estimates is limited by their large standard errors, they indicate that some genetic progress can be made in lamb performance from selection on sire 100-day weight with artificial rearing.

The experimental design required 16 pairs of high and low 100-day weight rams (trait 1) with 30 progeny per ram, in order to detect a statistically significant ( $P < 0.05$ ) co-heritability for growth traits of naturally reared progeny (trait 2), with a 0.80 probability ( $h^2_1 = 0.20$ ,  $h^2_2 = 0.10$ ,  $r_A = 0.90$ ) and a design selection differential of 3.0 s.d. units. This is equivalent to selecting the extreme 0.16 of high- and low-weight rams. In practice, using the adjusted ram-weight data, the maximum selection differential possible would have been 2.4 s.d. units, equivalent to selecting the extreme 0.28 of high- and low-weight rams. However, the selection differential was 1.7 s.d. units, which was essentially equivalent to choosing the high-weight rams at random from rams heavier than the mean weight, and similarly for low-weight rams. Selecting low-weight rams with an equal average deviation from overall mean weight as the high-weight rams proved difficult, as some of the low-weight rams died or failed to mate successfully. These rams were replaced, with the result that the selection differential was reduced. Similar problems were reported by Owen et al (1978).

Performance testing of ram lambs with artificial rearing

has been reported by Broadbent and Watson (1967) and by Owen et al. (1978), both using Suffolk rams. No selection was practised by Broadbent and Watson (1967) as only 15 rams were performance tested. Owen et al. (1978) reported a co-heritability estimate for lamb weight of 0.27 (s.e. 0.06) (trial 2, year 1: fitting source of sire) and recommended selection following artificial rearing for improvement in lamb growth. As their co-heritability estimate was significantly higher than the estimate from this study, it may be useful to compare the details of the two trials (Table 3.5), (the 1st year of the second field trial of Owen et al. (1978) was used, as source of rams was confounded in the first field trial).

The different regression coefficients and accordingly different mean squares for ram family means from the two studies are unlikely to be attributable to management/environmental differences as the ram weights under artificial rearing and the progeny weights under natural rearing were similar in the two trials, as were the phenotypic variances for ram weight and for progeny weight. The Texel-Oxford and Suffolk crosses have similar growth rates over the period studied (see Chapter 2) and the purebreeds have similar mature weights (93 and 91 kg respectively). Although the Texel-Oxford crosses were proportionately (0.02) heavier at 16 weeks than the Texel crosses, the difference did not approach statistical significance ( $P > 0.25$ ).

The magnitude of the selection differentials has no effect on the estimation of the regression coefficient, though it does affect the precision of the estimate. Despite the larger number of rams performance tested and rams selected in this trial the

TABLE 3.5

Comparison of this study with the second field trial of Owen, Brook  
Read, Steane and Hill (1978)

Terminal sire breed	Present study		Owen et al.
	Texel-Oxford	Texel	Suffolk
No. of rams tested	174		86
Proportion (number) selected	0.120 (41)		0.12 (20)
Mean weight (kg) (age in days) at selection	36.3 (100)		39.0 (95)
Slaughter weight s.d. (kg)	4.4		4.4
Selection differential (kg)	7.5		12.0
Mean number of progeny per ram	26		28
Mean weight of progeny (kg)	32.5 (27.5) <sup>+</sup>		33.0 <sup>++</sup>
Residual s.d. of progeny within sires (kg)	3.9 (3.5) <sup>+</sup>		4.4 <sup>++</sup>
Mean square for ram family means	11.6 (5.4) <sup>+</sup>		43.7 <sup>++</sup>
d.f.	34 (34) <sup>+</sup>		9 <sup>++</sup>
Regression coefficient on ram weight (kg/kg)	0.034 (0.032) <sup>+</sup>		0.135 <sup>++</sup>
s.e.	0.038 (0.034) <sup>+</sup>		0.033 <sup>++</sup>

+ Progeny traits at 112 ( $\frac{\text{days}}{84}$ ) of age.

++ Progeny traits at a combination of 84 and 113 days of age.

precision of the estimates was no better than that found by Owen et al (1978) due to the lower selection differential. The observed standard errors of the co-heritabilities for the two studies were as expected, using the formula of Hill (1970), given the selection differentials and number of rams performance tested and selected.

There seems no obvious explanation for the difference between the co-heritability estimates for lamb weight from the two trials. Recent heritability estimates of weight for age with natural rearing have been low (e.g. 0.04 (s.e. 0.04) (Wolf et al, 1981)) and the paternal half-sib heritability estimate from this trial was 0.09 (s.e. 0.06), adjusted to take account of the bias due to selection of the rams (Robertson, 1977). In retrospect, the estimate of Owen et al. (1978) seems rather high. However, it should be noted that the regression coefficients of progeny field performance on ram station performance from the 2 years of trial 2 of Owen et al (1978) were 0.135 (s.e. 0.033) and 0.064 (no s.e.), when source of sire was fitted, even though 10 of the 20 rams used in the 1st year, were used in both years. If the genetic correlation for progeny field performance with ram station performance is significantly less than 1, then the co-heritability estimate may be lower than expected, due to the interaction between station and field performance. Such interactions have been common for growth rate in other species (e.g. Baker, Wickham and Morris (1982) in beef cattle and Standal (1984) in pigs).

For artificial rearing to be effective, the co-heritability ( $r_A h_1 h_2$ ) must be higher than the heritability for natural rearing ( $h^2_2$ ). For example, the co-heritability estimate of 0.27 from Owen



et al (1978; trial 2, fitting source of sire) could be achieved if there was no interaction ( $r_A=1.0$ ), and would require  $h^2_1=0.73$  and  $0.36$  given  $h^2_2= 0.10$  and  $0.20$ , respectively. These values would be multiplied by  $1/r^2_A$  for  $r_A < 1.0$ , giving extremely high values for  $h^2_1$  as  $r_A$  falls. Therefore, the results of this trial may be more realistic and consistent with other genetic parameter estimates for early lamb growth than those of Owen et al (1978).

In the experiment, the co-heritability was similar to the heritability for natural rearing, which suggests that the advantage of reducing maternal effects on performance test is offset by the genetic correlation for natural and artificial rearing being markedly less than 1. Therefore, on the basis of this study, selection on ram 100-day weight with artificial rearing may not offer any advantage over natural rearing for improvement in lamb growth and carcass traits.

## SUMMARY

Forty-one Texel and Texel-Oxford sires were selected over 5 years (1978-82) on high and low adjusted 100-day weight from 174 ram lambs artificially reared from birth and performance tested. The correlated responses to selection were measured in 1103 crossbred progeny, out of an experimental group of crossbred ewes, the progeny being naturally reared in field conditions. Hierarchical analysis of variance was performed, fitting the usual fixed effects and interactions. Co-heritabilities ( $r_A h_1 h_2$ ;  $r_A$  is the genetic correlation between traits with heritabilities  $h_1^2$  and  $h_2^2$ ) were estimated from offspring-parent regression and from the realized responses to selection. The selection differentials achieved (1.70 standard deviations in 100-day weight between high- and low-weight sires) were lower than expected, due to mating difficulties, mortality and other requirements for the stock. The co-heritabilities for growth traits were generally positive but small (mean 0.08; s.e. 0.08). Though not statistically significant, lambs slaughtered at a fixed weight from the high-weight rams were slaughtered earlier with lighter and leaner carcasses, as expected. Similarly, lambs slaughtered according to fat cover from high-weight rams were slaughtered later with heavier slaughter and carcass weights. Generally, the co-heritabilities for carcass traits were not significantly different from zero for either slaughter group. On the basis of these results, selection on ram 100-day weight with artificial rearing may not offer any advantage over natural rearing in the improvement of lamb growth and carcass traits.



## CHAPTER 4

### ESTIMATION OF CARCASS LEANNESS IN YOUNG RAMS

#### INTRODUCTION

Excess fat production in British sheep carcasses in 1977 was estimated as 25,000 t, about 14% of the total carcass weight produced (Kempster, 1979). The Meat Promotion Executive of the Meat and Livestock Commission (MLC) reported that consumers found lamb the least versatile, fattest and most wasteful of meats (Kempster, 1983). Such waste fat production may be reduced by within-breed selection for leanness facilitated by an effective method of estimating body composition in rams before breeding age. Techniques for live-body measurement in sheep have been reviewed recently by Alliston (1983).

The use of different ultrasonic techniques for predicting carcass composition in sheep has been studied previously by several groups, but it is not always clear whether adjustments for lamb age and weight at the time of assessment were made. The Scanogram was evaluated by Pattie, Thompson and Butterfield (1975) and they concluded that it was of little value in predicting carcass lean content, although it did have some value in predicting fat content. Shelton, Smith and Orts (1977) scanned Rambouillet rams with the Scanogram and found correlations for total fat trim with ultrasonic fat thickness and eye muscle area of 0.47 and 0.45 respectively. Gooden, Beach and Purchas (1980) reported a correlation of 0.76 between ultrasonic measurements and carcass fat content using a

modified 'A' mode scanner. The Danscanner and Scanogram were compared for predicting both carcass lean and subcutaneous fat content by Kempster, Arnall, Alliston and Barker (1982). The proportional reduction in the residual m.s. on using the ultrasonic measurements of fat area for the Danscanner and Scanogram were 0.17 and 0.31 for carcass lean (g/kg) (residual m.s. = 1480) and 0.24 and 0.51 for subcutaneous fat (residual m.s. = 990) respectively. The current report provides more information on the Danscanner and Scanogram and evaluates another scanner, the Vetscan (Fischer Ultrasound Ltd., Edinburgh).

The relationship between plasma triglyceride concentrations and body fat content was also studied. In broilers, Griffin, Whitehead and Broadbent (1982) reported a phenotypic correlation of 0.38 between plasma triglyceride concentration and fat content. Triglyceride content of plasma very low density lipoprotein (VLDL) and low density lipoprotein (LDL) also showed reasonable correlations with fat content. Selection of male broilers on the basis of VLDL and LDL concentrations produced groups with significant differences in body fat content but little difference in body weight. However, the site of lipogenesis in poultry (liver) is different from that in sheep (adipocyte). Appreciating this, it was hoped that in rams, different amounts of body fat may be reflected in differential rates of fat mobilisation on fasting, as detected by plasma VLDL concentrations. The VLDL concentration may indirectly be indicative of carcass leanness as carcass lean and fat proportions are highly correlated (Wolf, Smith, King and Nicholson, 1981).

## MATERIAL AND METHODS

The comparisons were made on 36 Texel-Oxford young rams born in 1983 on the Animal Breeding Research Organisation's (ABRO) experimental farm at Blythbank, Tweeddale. The Texel-Oxford line was derived at ABRO from three to four generations of interbreeding of a Texel-Oxford cross. The dams of the rams were 1, 2, 3 or 4 years old at lambing with an even distribution over ages. Lambing took place from mid-March to mid-April (average lambing day of year = 92). Nine sires were used, seven 2-year-olds and two 1-year-old. The rams were artificially reared and housed from birth with individual food intakes and live weights recorded from 6 weeks of age for a period of 10 weeks. They were all slaughtered at the end of August (day 240 of the year).

Ultrasonic measurements were taken using the Vetscan and Danscanner on days 194 and 222 and the Scanogram on day 229. A single experienced operator used each machine. Details of ultrasonic scanning of sheep using the Danscanner and Scanogram are given by Kempster et al. (1982). Wool was clipped from the scanning site and liquid paraffin used to ensure acoustic contact. Scans were taken of the cross-section of the m. longissimus dorsi and overlying fat at the 12th rib. Tissue boundaries were identified on the scan photographs and the following measurements taken; fat depth: fat thickness measured over the m. longissimus dorsi 3.5cm (FD3), 6.0 cm (FD6) from the dorsal mid line and at the dorso-lateral corner of the muscle (FDK); fat area: fat area over the m. longissimus dorsi (MA).

All the above measurements were taken with the Danscanner and Scanogram, while the Vetscan measured the fat depths, FD6 and FDK, and muscle depth. The Danscanner's fat depth and fat area measurements included skin thickness whereas measurements of the Scanogram and Vetscan did not. Kempster et al (1982) reported that Danscanner ultrasonic measurements, both including and excluding skin thickness, had similar residual s.d. when used as predictors of carcass lean content.

For a 6-day plasma sampling period, starting on day 230, the rams were weighed and bled daily. Plasma VLDL and non-esterified fatty acid (NEFA) concentrations were determined from frozen samples at the end of the test period. On days 1 and 2 of sampling, the rams were fed normally, with straw being fed on day 3. The rams were fasted on days 4 and 5 and then fed normally on day 6. Four days after the end of the test, the rams were slaughtered.

The rams were slaughtered at a mean age of 21 weeks and mean live weight of 42.4kg. Half carcasses were dissected at the East of Scotland College of Agriculture (ESCA). They were cut into eight standard joints using anatomical reference points (Cuthbertson, Harrington and Smith, 1972) and each joint was dissected into lean, subcutaneous fat, intermuscular fat, bone and waste.

The data were standardised by fitting effects of dam age and birth type; live weight and age at time of measurement were fitted as covariates. The repeatability of ultrasonic measurements was calculated as the residual correlation between measurements. The value of individual ultrasonic measurements, food conversion

efficiency (g live-weight gain per kg food intake), NEFA and VLDL concentrations in estimating carcass leanness was assessed by the additional reduction in the residual m.s. after fitting the measurement as a covariate. This is equivalent to testing the significance of the regression coefficient of carcass leanness on the measurement.

The rams examined were those remaining after high and low truncation selection for 100-day weight (trait X), as required for another experiment (see Chapter 3). The effect of stabilizing selection (on the remainder) on the correlation of trait Y (ultrasonic fat depth) and Z (carcass leanness) is noted in the appendix.

## RESULTS

Means and standard deviations of ultrasonic measurements for the Danscanner, Scanogram and Vetscan are given in Table 4.1. The proportional increase in fat and muscle depths measured was approx. 0.10, from day 194 to day 222, as detected by the Danscanner and Vetscan. The repeatability of Danscanner and Vetscan fat depth measurements were similar, as were measurements of muscle depth. The change in fat and muscle areas measured did not follow a consistent pattern over the same period of time. The repeatability of muscle area and muscle depth were lower than for fat depth measurements.

The reductions in the residual m.s. of carcass leanness after fitting the fixed effects and covariates are given in Table 4.2. The base residual m.s. of 628 was used to assess the value of

TABLE 4.1

Means and standard deviations of fat area (FA), muscle area (MA) and fat depth (FD) as measured by the Danscanner, Scanogram and Vetscan ultrasonic machines and repeatabilities

Mean and (s.d.)	Day of year	Fat area (mm <sup>2</sup> )		Muscle area (mm <sup>2</sup> )	Fat depth (mm)			Muscle depth (mm) MD
		FA6	FAK		MA	FD3	FD6	
Danscanner+	194	500 (73)	674 (132)	1372 (240)	7.3 (1.4)	7.4 (1.2)	9.2 (1.8)	24.7 (3.2)
	222	525 (51)	630 (88)	1272 (158)	8.1 (1.0)	8.0 (1.3)	10.6 (1.8)	27.7 (2.5)
Scanogram	229	155 (39)	235 (62)	1276 (216)	2.8 (0.6)	3.3 (0.8)	4.1 (0.9)	20.2 (3.3)
Vetscan	194					1.8 (0.8)	1.8 (0.9)	23.0 (3.5)
	222					1.9 (0.8)	1.9 (0.9)	25.6 (2.3)
Repeatability <sup>++</sup>								
Danscanner								
within day	222	0.60	0.84	0.71	0.69	0.63	0.39	0.62
between days		0.48	0.40	0.16	0.55	0.39	0.53	0.27
Vetscan								
between days					0.43		0.40	0.28

+ Average of two measurements

++ Adjusted for fixed effects, lamb weight and age (s.e. = 0.18)



TABLE 4.2

Reduction in the residual m.s. of carcass leanness  
(g/kg) after fitting fixed effects with lamb  
age and weight as covariates

	Carcass leanness
No. of observations	36
Mean value	553.5
Residual m.s.	1109
Effects included in model	Residual m.s.
Fixed effects	758
Fixed effects and lamb age	784
Fixed effects and lamb weight	652
Fixed effects and lamb weight and age	628

the various predictors of carcass leanness. The proportional reduction in the residual m.s. of carcass leanness on including individual ultrasonic measurements in the model are given in Table 4.3. If the residual m.s. was proportionally reduced by less than 0.01, the ultrasonic measurements are not included in the Table. The Scanogram measurements were of little value in indicating carcass leanness, as shown by their absence in Table 4.3. For the Danscanner, the fat area measurements were better indicators of carcass leanness than were the fat depths and muscle measurements. However, the Vetscan fat depth measurements provided the best estimate of carcass leanness, by reducing the residual m.s. by about 20%, corresponding to a correlation of -0.45.

The means and standard deviations of plasma VLDL and NEFA concentrations and cumulative food conversion efficiency over the 10-week period are given in Table 4.4. The plasma VLDL concentrations rose on fasting but fell back to normal on refeeding. The plasma NEFA concentrations rose substantially on fasting and were still elevated at slaughter. Cumulative food conversion efficiency was variable in the first 2 weeks of test, but then remained constant for 4 weeks, and gradually declined for the remaining 3 weeks of test. The proportional reduction in the residual m.s. was less than 0.01 when any of these measurements were included in the model, so they were of little value as indicators of carcass leanness.

TABLE 4.3

Proportional reduction in the residual m.s. for carcass leanness by including ultrasonic measurement in the model<sup>+</sup>

	Day	Fat area (mm <sup>2</sup> )			Fat depth (mm)		
		FA6	FAK	FD3	FD6	FDK	(FD6+FDK)/2
Danscanner	194	11 <sup>++</sup>	0	5	2	0	
	222	12 <sup>++</sup>	15 <sup>++</sup>	3	12 <sup>++</sup>	3	
Vetscan	194				29 <sup>++</sup>	13 <sup>++</sup>	23 <sup>++</sup>
	222				14 <sup>++</sup>	20 <sup>++</sup>	18 <sup>++</sup>

<sup>+</sup> After fitting fixed effects with lamb age and weight as covariates.

<sup>++</sup> Regression coefficient of carcass leanness with ultrasonic measurement statistically significant from zero (P < 0.05)

TABLE 4.4

Means and standard deviations of plasma very low density lipoprotein (VLDL) and non-esterified fatty acid (NEFA) and cumulative food conversion efficiency

	Day of test						Week of test								
	1	2	3	4	5	6	1	2	3	4	5	6	7	8	9
VLDL <sup>+</sup>	28.7	31.7	35.8	38.4	37.2	28.0	217	322	305	303	306	301	285	274	269
s.d.	10.6	12.3	12.7	10.6	10.3	10.1									
NEFA <sup>+</sup>	37.0	30.6	276.0	601.9	658.0	735.3	217	322	305	303	306	301	285	274	269
s.d.	27.9	24.4	133.3	183.1	153.3	127.9									
Cumulative food conversion efficiency <sup>++</sup>							217	322	305	303	306	301	285	274	269
s.d.							226	87	64	45	35	37	33	31	28

<sup>+</sup> Plasma VLDL and NEFA concentrations measured in mmol/l x 100

<sup>++</sup> Cumulative food conversion efficiency, from 6 to 16 weeks of age, measured in g live-weight gain per kg food intake.

## DISCUSSION

For estimation of carcass leanness from measurements on the live animal, the average of the Vetscan fat depth (VFD) measurements gave the best estimate here, reducing the residual m.s. by 0.20. This held for the measurements on two occasions, so the results were repeatable. However, it should be noted that earlier published results with the Scanogram were encouraging (Kempster et al 1982), but these were not supported in this trial. It is important to confirm the present results of the Vetscan in another set of material. The results may be improved by scanning the rams at heavier weights, as fat depth would be greater and differences may be easier to detect. In practice, the estimation of carcass leanness could be improved by taking several independent measurements on each ram, at two or more locations on two or more occasions.

At present, there is little financial incentive to produce leaner lamb carcasses in the United Kingdom, though there is much industry concern about overfatness. Current selection in terminal sire breeds is mainly for growth rate (MLC, 1983). Future requirements in terminal sire breeds seem to be for fast growing leaner animals, as with pigs and cattle. Estimated genetic responses in average daily gain (ADG) and carcass leanness from selecting directly on each trait and by index selection are given in Table 4.5. Estimates of the phenotypic and genetic correlations and heritabilities for ADG and carcass lean proportion were obtained from Wolf et al (1981). The genetic correlation of VFD and ADG

TABLE 4.5

Estimated responses from selection on different traits<sup>+</sup> assuming equal selection intensities

Response	Selection on a single trait		Selection index to improve		
	ADG <sup>++</sup>	VFD <sup>+++</sup>	ADG	Lean <sup>\$</sup>	Lean+ADG
ADG	0.10 <sup>\$\$</sup>	0.02	0.10	0.05	0.08
Lean	0.03	0.13	0.06	0.13	0.12

+ Response is expressed in multiples of the phenotypic s.d. and selection intensity i.  
 ++ ADG: average daily gain from birth to slaughter.  
 +++ VFD: Vetscan fat depth  
 \$ Lean: carcass lean proportion  
 \$\$ Estimates of heritability (on diagonal) and correlations phenotypic (above) and genetic below

	ADG	VFD	Lean
ADG	0.10	0.00	0.08
VFD	-0.22	0.12	-0.45
Lean	0.15	-0.58	0.41

and carcass leanness were derived from Wolf et al (1981) with adjustments for the ultrasonic measurements. The corresponding phenotypic correlations for VDF used were from the current data. A heritability of ultrasonic fat depth of 0.12 was reported by Bennett, Rae, Clarke and Kirton (1983). Growth rate and leanness were given equal economic weights to form a simple index since it is difficult to derive future economic weights for these traits. With this selection index, appreciable responses can be obtained in both traits. However, derivation of future economic weights for terminal sire breeds is required for calculation of an economic index. On a national scale, even small changes in carcass leanness in nucleus flocks of terminal sire breeds by the use of ultrasonics would provide substantial benefits to the meat industry, of the order of £0.1 million per annum by reducing the proportion of waste fat produced by 0.01 (Kempster, 1979).

## SUMMARY

The accuracy of six methods to estimate carcass leanness in young rams was studied in 36 Texel-Oxford rams, measured at 5 months of age. The rams were slaughtered and dissected. Plasma non-esterified fatty acid and very low density liprotein concentrations, sampled before, during and after fasting showed no relationship with carcass leanness. The same was true for food conversion efficiency measured from 6 to 16 weeks of age, and for measurements taken with the Scanogram ultrasonic machine. The Vetscan and Danscanner ultrasonic machines gave repeatable measurements of fat depth (0.41 and 0.46 respectively). The Vetscan was the best predictor of carcass leanness by proportionally reducing the residual mean square by about 0.20, corresponding to a correlation of -0.45 between ultrasonic fat depth and carcass leanness. Inclusion of average daily gain and ultrasonic fat depth in a selection index would allow appreciable improvements in both traits.



## APPENDIX

Bias in the correlation of Y and Z with stabilizing selection on X. Let p be the proportion of the population beyond each truncation threshold and

V be the population variance before selection. If

$V_t$  is the variance of the remaining mid-population group, then

$$(1-2p)V_t + 2p [1-i(i-x) + i^2]V = V$$

where  $\pm x$  is the truncation point

and  $\pm i$  are the means of the selected individuals.

This reduces to

$$\begin{aligned} V_t &= V[1 - 2ipx/(1-2p)] \\ &= V[1 - s]. \end{aligned}$$

Let  $V_{yt}$  be the population variance of trait Y after stabilizing selection on trait X, then

$$V_{yt} = V_y - (\text{cov}_{yx}^2/V_x)s$$

and

$$\begin{aligned} \text{cov}_{ytzt} &= \text{cov}_{yz} - (\text{cov}_{yx} \text{cov}_{zx}/V_x)s \\ &= \text{cov}_{zyz} [1 - (r_{yx}r_{zx}/r_{yz})s]. \end{aligned}$$

Therefore

$$\begin{aligned} V_{yt} &= V_y[1 - r_{yx}^2 s] \\ V_{zt} &= V_z[1 - r_{zx}^2 s] \\ r_{ytzt} &= (r_{yz} - r_{yx}r_{zx}s) / \sqrt{(1 - r_{yx}^2 s)(1 - r_{zx}^2 s)}. \end{aligned}$$

In the context of the trial, the equation could be used as follows: stabilizing selection on 100-day weight (trait X); correlation of carcass leanness (trait Z) with Vetscan fat depth (trait Y).

## CHAPTER 5

### DESIGN OF MULTIVARIATE SELECTION EXPERIMENTS TO ESTIMATE GENETIC PARAMETERS

#### INTRODUCTION

Precise, unbiased estimates of genetic parameters, such as heritability and genetic correlations, are necessary to optimise breeding programs and to predict rates of change for various selection schemes. These parameters can be estimated from the covariance among collateral relatives or from the regression of the progeny performance on that of their parents. Appropriate equations for the variances of these estimates obtained by such methods are well documented (e.g. Falconer, 1981). Equations for calculating the variance of heritability estimates derived from single-trait selection experiments for various designs have been derived by Hill (1971).

One experimental design objective in single-trait selection experiments is to minimise the variance of the heritability estimate which is influenced by factors such as population size, selection intensity, family size, the genetic and phenotypic parameters and the number of generations of selection. Using prior information about the parameters of interest, efficient selection experiments can be designed to obtain precise, unbiased estimates of the parameters using the equations of Hill (1971).

When dealing with two or more traits, the genetic variances and covariances are parameters of interest and, as Thompson (1976) has noted, it is not obvious what the optimal design objective

should be. Robertson (1959) and Tallis (1959) discussed the sampling variance of the genetic correlation coefficient and suggested that designs which are efficient for heritability estimation are also efficient for estimation of genetic correlations. For two traits, individuals in the parental generation could be split into two groups, selecting high and low within one group for trait  $X_1$  and selecting high and low within the other group for trait  $X_2$  (Reeve, 1955) and studying either the regression of offspring traits on traits of the selected parents or the direct and correlated responses to selection. However, this may not be the most efficient design in an overall sense. Indices using both traits could be used as the selection criteria, rather than selecting directly on the traits measured. However, Gunsett *et al* (1984) suggest a strong dependency of the design efficiency on the index weights used. These techniques for estimating genetic variances and covariances for two traits and the efficiencies of different selection designs are discussed. Two generation selection experiments when parental observations are only taken on one sex are considered in detail. A different experimental design to the classical high-low individual selection method is examined and it is shown to be more efficient and robust.

#### OPTIMALITY CRITERIA

Given a regression problem,  $Y = X\beta + e$ , where  $Y$  is a vector of the dependent variable,  $X$  is the design matrix for the independent variables and  $e$  is the vector of residuals with variance-covariance matrix  $V$ , then the confidence ellipsoid of the

generalised least squares estimate  $\hat{\beta}$  of  $\beta$ ,

$\hat{\beta} = (X'V^{-1}X)^{-1}X'V^{-1}Y$ , with variance  $(X'V^{-1}X)^{-1}$ , has the form

$$[\beta : (\beta - \hat{\beta})' X'V^{-1}X (\beta - \hat{\beta}) < \text{constant}]$$

for any specified confidence coefficient. The content of the ellipsoid (e.g. volume in three dimensions) is proportional to  $|X'V^{-1}X|^{-1/2}$ . Therefore one design criterion is to minimise the content of the ellipsoid or to maximise  $|X'V^{-1}X|$ , the D-optimality criterion (Silvey, 1980). The determinant of  $X'V^{-1}X$  will be denoted by  $\text{DET}(\beta)$ . The D-optimality criterion has the useful invariance property that if a design  $X$  maximises  $\text{DET}(\beta)$ , then the same design  $X$  also maximises  $\text{DET}(T^*\beta)$ , where  $T^*$  is a full rank transformation matrix. Therefore, a design that is optimal for estimation of  $\beta$  is also optimal for a linear transformation,  $T^*\beta$ , of  $\beta$ . There are other overall criteria; for example, to maximise the trace of  $X'V^{-1}X$  (the sum of the diagonal elements of the matrix) or to maximise the minimum eigenvalue of  $X'V^{-1}X$ , but these do not have this invariance property.

#### STANDARDISATION OF TRAITS

The genetic and phenotypic variance-covariance matrices for the traits will be denoted by  $G$  and  $P$  respectively. Cases of standardised traits, with mean zero, when the diagonal elements of the  $P$  matrix are equal to one are considered and that the traits are normally distributed is assumed. The methods and designs considered can be applied to multivariate data but are developed using bivariate data. The genetic variances and covariances of the standardised traits are then heritabilities ( $h_1^2$  and  $h_2^2$ ) and co-heritabilities ( $r_A h_1 h_2$  where  $r_A$  is the genetic correlation between

the two traits). In the estimation of these parameters, it is convenient to work in terms of the vector  $\beta' = 0.5[h_1^2 \quad r_A h_1 h_2 \quad h_2^2]$  rather than the (2x2) symmetric matrix of genetic variances and covariances.

There is no loss of generality from standardising the traits, for if the diagonal elements of the P matrix are not equal to one, then the phenotypic variables can be standardised using a transformation,  $T^*$ , with the result that the genetic variance-covariance matrix of the transformed variables is  $T^*GT^{*'}.$  The invariance argument for D-optimality shows that a D-optimal design for the parameter  $\beta$  is also D-optimal for the parameters in  $T^*GT^{*'}.$

Further, it is assumed that errors in the phenotypic matrix P can be neglected, either because there is adequate previous data or parental data on which to base estimation of P. The emphasis, within this paper, is on comparing estimation procedures and suggesting designs for genetic parameter estimation and so this assumption should have a negligible effect on the conclusions. Certainly, the formulation leads to known results on univariate heritability estimation.

## ESTIMATION AND DESIGN FROM RESPONSE TO DIVERGENT

### TRUNCATION SELECTION

A common method of estimating genetic parameters for two traits, from divergent truncation selection experiments, is to have two selection groups using a different selection index in each group and measure the selection differentials and the correlated responses for the two traits on both selection indices (Falconer, 1981). For

each of the selection indices,  $I_m$  ( $m=1,2$ ), assume a total of  $M$  unrelated individuals are measured for both traits and a proportion  $p$  with the highest and  $p$  with the lowest index values are selected, such that  $pM = N$ . A total of  $R$  progeny are reared and recorded and with equal family sizes there are  $n = R/2p$  progeny per family. Let  $i$  and  $x$  be the expected selection differential and abscissa on the standardised normal curve corresponding to  $p$  and assume equal selection differentials in the two groups. Note that the upper and lower cases of the letter  $I$  denote different parameters, however this is standard notation (Falconer, 1981).

Initially alternative estimation procedures and designs will be considered for fixed experimental resources. Later, optimisation of the selection proportion,  $p$ , family size,  $n$ , and the relative proportion of offspring generation measurements to parental generation measurements,  $R$ , will be discussed.

It is of interest to consider the possible combinations of selection weights for the two indices. If a selection index  $I_m = b_{1m}x_1 + b_{2m}x_2$ , then

$$I_m \equiv (b_{1m}/\sqrt{b_{1m}^2 + b_{2m}^2})x_1 + (b_{2m}/\sqrt{b_{1m}^2 + b_{2m}^2})x_2 = x_1 \cos\theta_m + x_2 \sin\theta_m$$

selects the same individuals, where  $x_j$  and  $b_{jm}$  are the standardised phenotypic values and index weights of the  $j^{\text{th}}$  trait for the  $m^{\text{th}}$  index respectively and  $\tan\theta_m = b_{2m}/b_{1m}$ . Each selection index is characterised by a single parameter  $\theta_m$ . By symmetry only the values of  $\theta_m$  in the range  $0^\circ$  to  $180^\circ$  need consideration. Graphically, the line  $x_1 \cos\theta_m + x_2 \sin\theta_m = 0$  makes an angle  $\theta_m$  with the  $x_1$  axis.

The expected genetic response,  $\Delta G_{jm}$ , in the progeny for trait  $j$  due to selection on index  $m$ , is given by the product of the

regression of the additive genotype of the  $j^{\text{th}}$  trait on the phenotype of the  $m^{\text{th}}$  index and the selection differential ( $SD_m$ ) of the  $m^{\text{th}}$  index. Thus  $\Delta G_{jm} = 0.5(b_{jm} \sigma_{jj} + b_{km} \sigma_{jk}) SD_m / \text{var}(I_m)$  where  $\sigma_{jj}$  and  $\sigma_{jk}$  are, respectively, the genetic variance for trait  $j$  and genetic covariance for traits  $j$  and  $k$  ( $j=1,2$ ;  $k=3-j$ ) and  $\text{var}(I_m)$  is the variance of the  $m^{\text{th}}$  index. The selection differential for the  $m^{\text{th}}$  index is calculated as the difference in mean index value between the high and low parental lines. The response in each trait can be estimated as the difference between the high and low progeny lines. The index weights  $b_{jm}$  are usually determined by biological arguments about the traits or the desired direction of the response (Eisen, 1977). The responses of trait  $j$  in selection group  $m$  can be written in the form of a regression model, regressing responses in the two measured traits on selection differentials of the indices.

$$\begin{bmatrix} \Delta G_{1m} \\ \Delta G_{2m} \end{bmatrix} = \begin{bmatrix} b_{1m} SD_m / \text{var}(I_m) & b_{2m} SD_m / \text{var}(I_m) & 0 \\ 0 & b_{1m} SD_m / \text{var}(I_m) & b_{2m} SD_m / \text{var}(I_m) \end{bmatrix} \beta + [e]$$

or  $Y = X\beta + e$ . The model can also be defined in terms of selection differentials for each measured trait ( $SD_{jm}$ ),

$$\begin{bmatrix} \Delta G_{1m} \\ \Delta G_{2m} \end{bmatrix} = \frac{1}{(1-r_p^2)} \begin{bmatrix} SD_{1m} - r_p SD_{2m} & -r_p SD_{1m} + SD_{2m} & 0 \\ 0 & SD_{1m} - r_p SD_{2m} & -r_p SD_{1m} + SD_{2m} \end{bmatrix} \beta + [e]$$

where  $r_p$  is the phenotypic correlation between the two traits.

Alternatively, using the expected value of  $SD_m$ , the expected value of the design matrix  $X$  can be conveniently written using the angles

$\theta_m$ ,

$$\frac{2i}{\sigma_{I_m}} \begin{bmatrix} \cos\theta_m & \sin\theta_m & 0 \\ 0 & \cos\theta_m & \sin\theta_m \end{bmatrix} \quad (1)$$

for each index, where  $\sigma_{I_m}$  is the standard deviation of the  $m^{\text{th}}$  index.

The residuals within lines are correlated, due to the family structure of the design, but there is no correlation of residuals between lines. The 4x4 variance-covariance matrix (V) of the residuals is therefore symmetric and block diagonal

$$V = f \begin{bmatrix} F & 0 \\ 0 & F \end{bmatrix} \quad (2)$$

The matrix F represents the 2x2 variance-covariance of a family mean after regressing on parental values and the factor f relates the variance of the mean genetic response for one index to the variance of a family mean. With response/selection differential estimation, there are N parents in each of the selected high and low lines, therefore  $f = 2/N$ .

The structure of F can be derived using the equations of Hill (1971) for the variance of residuals from single-trait selection. The variance for one progeny mean is

$$F = [(r_{oo}G - r_{op}GP^{-1}Gr_{op}) + (P - r_{oo}G)/n] \quad (3)$$

where  $r_{oo}$  and  $r_{op}$  are Wright's coefficients of relationship for progeny of the same parent and for progeny with parent respectively. Note that the first term in equation 3 is the variance of a family genotypic mean about the regression (drift variance) and the second term is the variance of measurement error in the family mean value. For example, in single-trait selection on parents of one sex with half-sib families

$$G = h^2, \quad P = 1.0, \quad r_{oo} = 0.25, \quad r_{op} = 0.5$$

and 
$$F = [0.25 h^2(1 - h^2) + (1 - 0.25 h^2)/n].$$



Gunsett et al (1982, 1984) gave similar formulae for V, however their genetic drift term does not include any genetic relationship parameters ( $r_{oo}$ ,  $r_{op}$ ) and their measurement error term does not have the divisor of the number of parents in each index.

Investigation of  $DET(\beta)$  and calculation of the inverse of V would be simpler if the matrix F was diagonal. As the matrix F is a function of the genetic and phenotypic variance-covariance matrices, transformation to independent traits would diagonalise F. Such a transformation exists and is often called a canonical transformation (Rao, 1973). Let  $S^*$  be the transformation matrix from the original scale to the canonical scale, such that

$$\begin{bmatrix} C_1 \\ C_2 \end{bmatrix} = S^* \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$

where  $C_1$  and  $C_2$  are the canonical traits which are phenotypically and genetically uncorrelated. Then  $S^*$  is such that  $S^*PS^{*'} = I$  equals the identity matrix and  $S^*GS^{*'} = G_C$  where  $G_C$  is the diagonal genetic variance-covariance matrix on the canonical scale. For half-sib family data, matrix  $F^{-1} = D$  becomes

$$D = \begin{bmatrix} d_1 & 0 \\ 0 & d_2 \end{bmatrix} \quad (4)$$

where  $d_j = (0.25\lambda_j(1 - \lambda_j) + (1 - 0.25\lambda_j)/n)^{-1}$  and  $\lambda_j$  denotes the canonical heritability of the  $j^{\text{th}}$  canonical trait.

If  $\beta_C$  is the vector of genetic parameters on the canonical scale, similar to  $\beta$ , and the indices on the canonical scale are  $I_1 = C_1\cos\theta_{C1} + C_2\sin\theta_{C1}$  and  $I_2 = C_1\cos\theta_{C2} + C_2\sin\theta_{C2}$ , where  $\theta_{C1}$  and  $\theta_{C2}$  are the angles of the canonical selection indices, then  $\sigma_{Im} = 1$  and  $X'V^{-1}X_C$ , the value of  $X'V^{-1}X$  for canonical traits is derived

from equations 1 to 4

$$X'V^{-1}X_C = \begin{bmatrix} d_1B_1 & d_1B_3 & 0 \\ d_1B_3 & d_1B_2 + d_2B_1 & d_2B_3 \\ 0 & d_2B_3 & d_2B_2 \end{bmatrix} \quad (5)$$

The expected value of  $DET(\beta_C)$  is

$$DET(\beta_C) = |X'V^{-1}X_C| = d_1d_2(d_1B_2 + d_2B_1)(B_1B_2 - B_3^2) \quad (6)$$

where  $B_1 = 2Ni^2 (\cos^2\theta_{C1} + \cos^2\theta_{C2})$

$$B_2 = 2Ni^2 (\sin^2\theta_{C1} + \sin^2\theta_{C2}) = 2Ni^2(2 - B_1) \quad (7)$$

$$B_3 = Ni^2 (\sin 2\theta_{C1} + \sin 2\theta_{C2})$$

It can be shown that  $DET(\beta) = (1-r_p^2)^{-3}DET(\beta_C)$  (see Appendix 1). In order to maximise  $DET(\beta_C)$ , it is differentiated with respect to  $B_2$  and  $B_3$ , and the maximum occurs when

$$\frac{B_2}{2Ni^2} = \frac{-2(d_1-2d_2) \pm 2\sqrt{d_1^2 - d_1d_2 + d_2^2}}{3(d_2-d_1)} \quad (8)$$

and  $B_3 = \sin 2\theta_{C1} + \sin 2\theta_{C2} = 0$ , therefore  $\theta_{C2} = \theta_{C1} + 90^\circ$  or  $\theta_{C1} + \theta_{C2} = 180^\circ$ .

There are two cases to consider when maximising  $DET(\beta_C)$ . If the canonical heritabilities are equal,  $d_1$  equals  $d_2$ , then the maximum value of  $DET(\beta_C)$  occurs when  $B_2/2Ni^2 = 1$  or  $\theta_{C2} = \theta_{C1} + 90^\circ$ . The indices on the canonical scale are  $I_1 = C_1\cos\theta_{C1} + C_2\sin\theta_{C1}$  and  $I_2 = C_2\cos\theta_{C1} - C_1\sin\theta_{C1}$  and this pair of axes are at right angles, the orthogonal design. The phenotypic covariance between the indices is zero. There are an infinite number of pairs of indices resulting in the maximum value of  $DET(\beta_C)$ .

If the canonical heritabilities are unequal, then  $\theta_{C1} + \theta_{C2} = 180^\circ$  and  $\theta_{C1}$  can be derived using equation 8 as  $B_2/2Ni^2 = 2\sin^2\theta_{C1}$ . The indices on the canonical scale are

$$I_1 = C_1 \cos \theta_{C_1} + C_2 \sin \theta_{C_1} \text{ and } I_2 = C_2 \sin \theta_{C_1} - C_1 \cos \theta_{C_1}.$$

The lines  $I_1 = 0$  and  $I_2 = 0$  are symmetric about the  $C_1$  and  $C_2$  axes, the symmetric design. Note that the angle between  $I_1$  and the  $C_1$  axis is equal to the angle between  $I_2$  and the  $C_1$  axis.

#### ESTIMATION AND DESIGN FROM OFFSPRING - PARENT REGRESSION

The heritability of a trait can be estimated from the regression of progeny performance on parent performance, rather than using a summary of parental information and responses to selection. The design of experiments to estimate the heritability of a trait using offspring-parent regression have been discussed by Hill (1970) and Hill and Thompson (1977).

Offspring-parent regression techniques can be used to estimate genetic parameters of more than one trait simultaneously. The standardised observations on two traits for the  $j^{\text{th}}$  parent and its offspring mean are defined as  $x_{1j}$ ,  $x_{2j}$  and  $\bar{o}_{x1j}$ ,  $\bar{o}_{x2j}$  respectively.

Then

$$\begin{aligned} \begin{bmatrix} \bar{o}_{x1j} \\ \bar{o}_{x2j} \end{bmatrix} &= 0.5 \text{ GP}^{-1} \begin{bmatrix} x_{1j} \\ x_{2j} \end{bmatrix} + [e] \\ &= 0.5 \text{ G} \begin{bmatrix} s_{1j} \\ s_{2j} \end{bmatrix} + [e] \\ &= \begin{bmatrix} s_{1j} & s_{2j} & 0 \\ 0 & s_{1j} & s_{2j} \end{bmatrix} \beta + [e] \end{aligned}$$

where  $s_{1j}$  and  $s_{2j}$  are  $(x_{1j} - r_p x_{2j}) / (1 - r_p^2)$  and  $(x_{2j} - r_p x_{1j}) / (1 - r_p^2)$  respectively.

Combining the information from all  $4N$  offspring-parent pairs,  $\beta$  can be estimated as before. The matrix  $V$  is now a  $8N \times 8N$  block diagonal matrix with the  $F$  matrix repeated  $4N$  times down the diagonal.

The contribution of each family to  $X'V^{-1}X$  can be expanded as

$$(X'V^{-1}X)_j = s_{1j}^2 \begin{bmatrix} D_{11} & D_{12} & 0 \\ D_{21} & D_{22} & 0 \\ 0 & 0 & 0 \end{bmatrix} + s_{1j}s_{2j} \begin{bmatrix} 0 & D_{11} & D_{12} \\ D_{11} & D_{12}+D_{21} & D_{22} \\ D_{21} & D_{22} & 0 \end{bmatrix} + s_{2j}^2 \begin{bmatrix} 0 & 0 & 0 \\ 0 & D_{11} & D_{12} \\ 0 & D_{21} & D_{22} \end{bmatrix} \quad (9)$$

where  $D_{jk}$  are the elements of  $F^{-1}$  (equation 3). The sums of squares and crossproducts of the parental traits, after selection, are calculated using

$$\begin{aligned} \text{cov}(x_1, x_2 \mid \text{selection on } I) &= \\ \text{cov}(x_1, x_2) - \frac{\text{cov}(x_1, I) \text{cov}(x_2, I)}{\text{var}(I)} + \frac{\text{cov}(x_1, I) \text{var}(I^*) \text{cov}(x_2, I)}{\text{var}^2(I)} & \\ = \text{cov}(x_1, x_2) + \frac{\text{ix cov}(x_1, I) \text{cov}(x_2, I)}{\text{var}(I)} & \quad (10) \end{aligned}$$

where  $\text{var}(I^*)$  is the variance of the index after selection. The sums of squares and crossproducts of  $s_{1j}$  and  $s_{2j}$ , after selection, can be determined from

$$\begin{bmatrix} \sum_{j=1}^{4N} s_{1j}^2 & \sum_{j=1}^{4N} s_{1j}s_{2j} \\ \sum_{j=1}^{4N} s_{1j}s_{2j} & \sum_{j=1}^{4N} s_{2j}^2 \end{bmatrix} = P^{-1} \begin{bmatrix} \sum_{j=1}^{4N} x_{1j}^2 & \sum_{j=1}^{4N} x_{1j}x_{2j} \\ \sum_{j=1}^{4N} x_{1j}x_{2j} & \sum_{j=1}^{4N} x_{2j}^2 \end{bmatrix} P^{-1} \quad (11)$$

As before, transformation on to the canonical scale results in the diagonalisation of the  $F$  matrix and  $X'V^{-1}X_C$  has the same structure

as in equation 5, where now

$$B_1 = \sum_{j=1}^{4N} C_{1j}^2, \quad B_2 = \sum_{j=1}^{4N} C_{2j}^2 \quad \text{and} \quad B_3 = \sum_{j=1}^{4N} C_{1j}C_{2j} \quad (12)$$

with  $C_{1j}$  and  $C_{2j}$  being the observations on the canonical scale of the  $j^{\text{th}}$  selected parent and a total of  $4N$  selected individuals as before.  $\text{DET}(\beta_C)$  becomes

$$\text{DET}(\beta_C) = d_1 d_2 (d_1 B_2 + d_2 B_1)(B_1 B_2 - B_3^2)$$

which is of the same form as equation 6, with  $B_1$ ,  $B_2$  and  $B_3$  given by equation 12 rather than equation 7. The expected sums of squares and cross-products of the observations can be rewritten as

$$B_1 = 2N[2 + ix(\cos^2\theta_{C1} + \cos^2\theta_{C2})]$$

$$B_2 = 2N[2 + ix(\sin^2\theta_{C1} + \sin^2\theta_{C2})]$$

$$B_3 = Nix[\sin 2\theta_{C1} + \sin 2\theta_{C2}]$$

Then

$$\text{DET}(\beta_C) = (2N)^3 d_1 d_2 [d_1(2+ixH) + d_2(2+ix(2-H))] [2+ixH] [2+ix(2-H)] \quad (13)$$

with  $H = \sin^2\theta_{C1} + \sin^2\theta_{C2}$ . In order to maximise  $\text{DET}(\beta_C)$ , it is differentiated with respect to  $B_2$  and  $B_3$ , and the maximum occurs when

$$H = \frac{-2 [(d_1 - 2d_2)ix - (d_1 + d_2)] \pm 2(2+ix)\sqrt{d_1^2 - d_1 d_2 + d_2^2}}{3ix(d_2 - d_1)} \quad (14)$$

and  $B_3 = \sin 2\theta_{C1} + \sin 2\theta_{C2} = 0$ , therefore  $\theta_{C2} = \theta_{C1} + 90^\circ$  or  $\theta_{C1} + \theta_{C2} = 180^\circ$ . If the canonical heritabilities are equal,  $d_1$  equals  $d_2$ , then  $H$  equals one and  $\text{DET}(\beta_C)$  is maximised when  $\theta_{C2} = \theta_{C1} + 90^\circ$ . This corresponds to a ridge of points where  $\text{DET}(\beta_C)$  is of constant value (the previously mentioned orthogonal design). If the canonical heritabilities are not equal a symmetric

design with  $2\sin^2\theta_{C_1} = H$ , found from equation 14, is again optimal.

The ratio of values of  $\text{DET}(\beta_C)$  from the orthogonal design using the offspring-parent regression and response/selection differential estimation is  $((2 + ix)/i^2)^3 > 1.0$ . For example, when  $p$  equals 0.10 and 0.20, the ratio equals  $(1.38)^3$  and  $(1.62)^3$  respectively. The proportional gain in precision  $(2+ix)$  from the offspring-parent regression designs comes from two sources. For example, if  $I_1 = C_1$  and  $I_2 = C_2$ , then  $(1 + ix)$  is proportional to the sums of squares for  $C_1$  from selection on  $I_1$  compared to  $i^2$  used in response/selection differential estimation. The remainder  $((2+ix)-(1+ix))$  is proportional to the sums of squares for  $C_1$  with selection on  $I_2$ , which is information not used in response/selection differential estimation.

Canonical traits have been used to simplify the development of the variance formulae and interpretation of the designs. When the experiment is being designed,  $G$  and hence the canonical transformation are not known precisely, therefore the specification of the optimal design is difficult. However, the class of orthogonal designs includes all pairs of indices that are phenotypically uncorrelated. On the standardised scale, an index  $I_2 = x_1\cos\theta_{C_2} + x_2\sin\theta_{C_2}$  can be found phenotypically uncorrelated to  $I_1 = x_1\cos\theta_{C_1} + x_2\sin\theta_{C_1}$ , if  $\tan\theta_{C_2} = -(1+r_p\tan\theta_{C_1})/(r_p+\tan\theta_{C_1})$ . This gives some flexibility in the choice of designs. For example, the three pairs of indices  $I_1 = x_1$  and  $I_2 = x_2 - r_px_1$ ,  $I_1 = x_2$  and  $I_2 = x_1 - r_px_2$  and also  $I_1 = x_1 + x_2$  and  $I_2 = x_1 - x_2$  are members of the class of orthogonal designs. This choice of indices can be made without "a priori" knowledge of  $G$  and is optimal if the canonical

heritabilities are equal.

Manipulation of equations 13 and 14 shows that the ratio of  $DET(\beta_C)$  using the optimal symmetric design compared with using one pair from the above three indices is  $(1+\eta\delta)/(1-\eta^2)$  with  $\eta = (-1 \pm \sqrt{1+3\delta^2})/3\delta = ix(H-1)/(2+ix)$  and  $\delta = (d_1-d_2)/(d_1+d_2)$ . For a range of canonical heritabilities, the ratio was generally less than 1.05. This suggests that the proportional increase in precision of a genetic variance or covariance estimate will be at most 0.02 ( $= (1.05)^{1/3} - 1$ ), from using the symmetric design compared with using the orthogonal design. Therefore efficient selection indices can be constructed without estimates of the genetic parameters being available.

To illustrate these results, Figures 1 and 2 show the contours for  $DET(\beta)$  estimated by response/selection differential (Figure 1) and offspring-parent regression (Figure 2). The heritabilities are 0.6 and 0.9 and the genetic and phenotypic correlations are 0.8 and 0.6 respectively, with 600 sires selected per index and a family size of 10 and selection proportion of 0.3, as used by Gunsett et al (1984). Included are lines indicating the orthogonal designs with the same value of  $DET(\beta)$  (the orthogonal design  $I_1 = x_1 + x_2$ ,  $I_2 = x_1 - x_2$  is denoted by O) and the symmetric designs (the optimal symmetric design is denoted by S). The classical design  $I_1 = x_1$ ,  $I_2 = x_2$  is denoted by C ( $\theta_1=0^\circ$ ,  $\theta_2=90^\circ$ ). The contour for the orthogonal designs in Figure 1 corresponds to the ridge noted by Gunsett et al (1984). When  $\theta_1 = \theta_2$  in Figure 1, then  $DET(\beta) = 0$  because only two parameters can be estimated. The orthogonal, symmetric and classical designs have values of  $DET(\beta)$

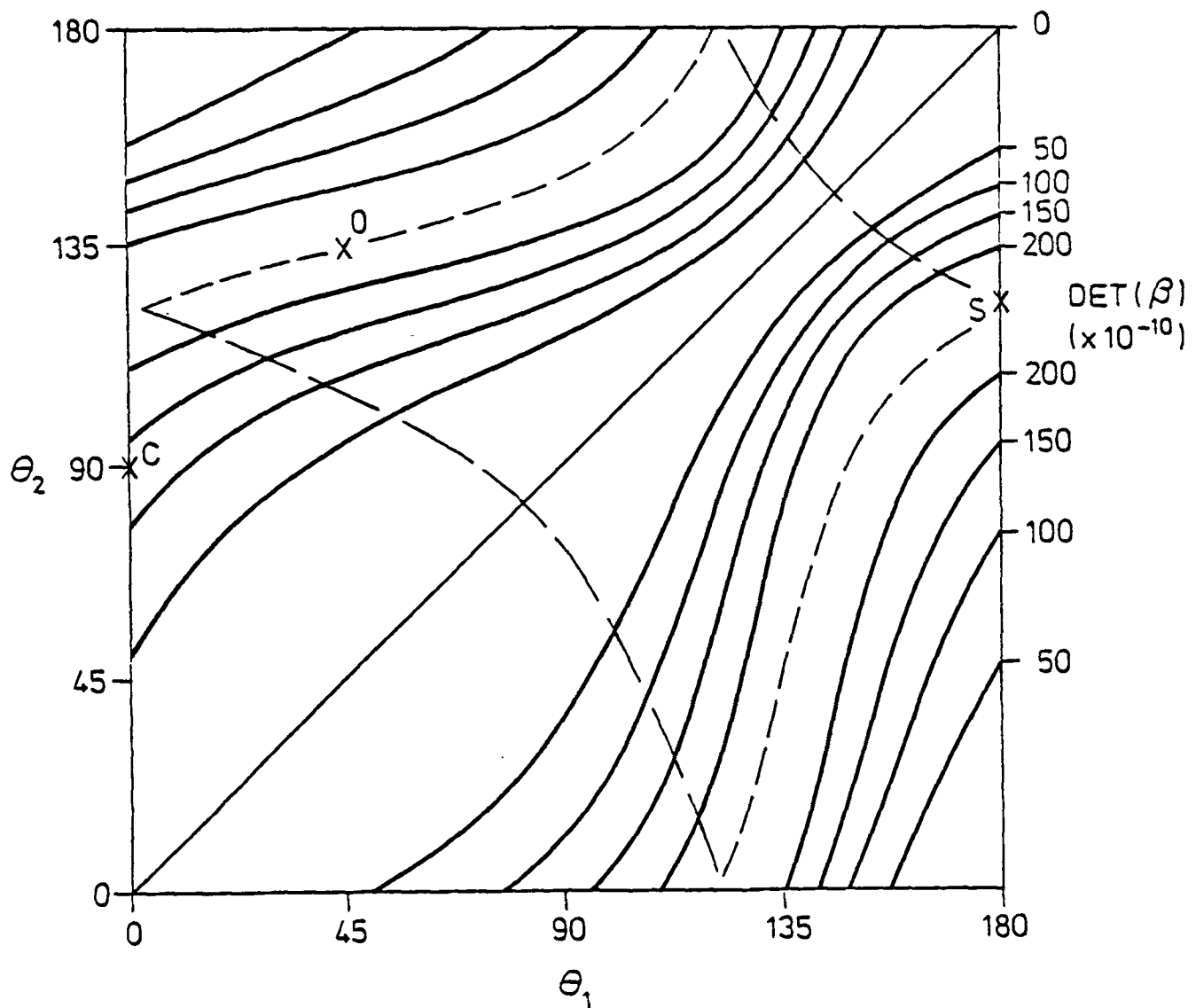


Figure 1 : Contours for  $\text{DET}(\beta)$  (divided by  $10^{10}$ ) for various linear indices of the traits defined by angles  $\theta_1$  and  $\theta_2$  with  $\beta$  estimated by response/selection differential. The classes of orthogonal designs (---), symmetric designs (—), the orthogonal design  $I_1 = x_1 + x_2$ ,  $I_2 = x_1 - x_2$  (O), the optimal symmetric design (S) and the classical design  $I_1 = x_1$ ,  $I_2 = x_2$  (C) are included.



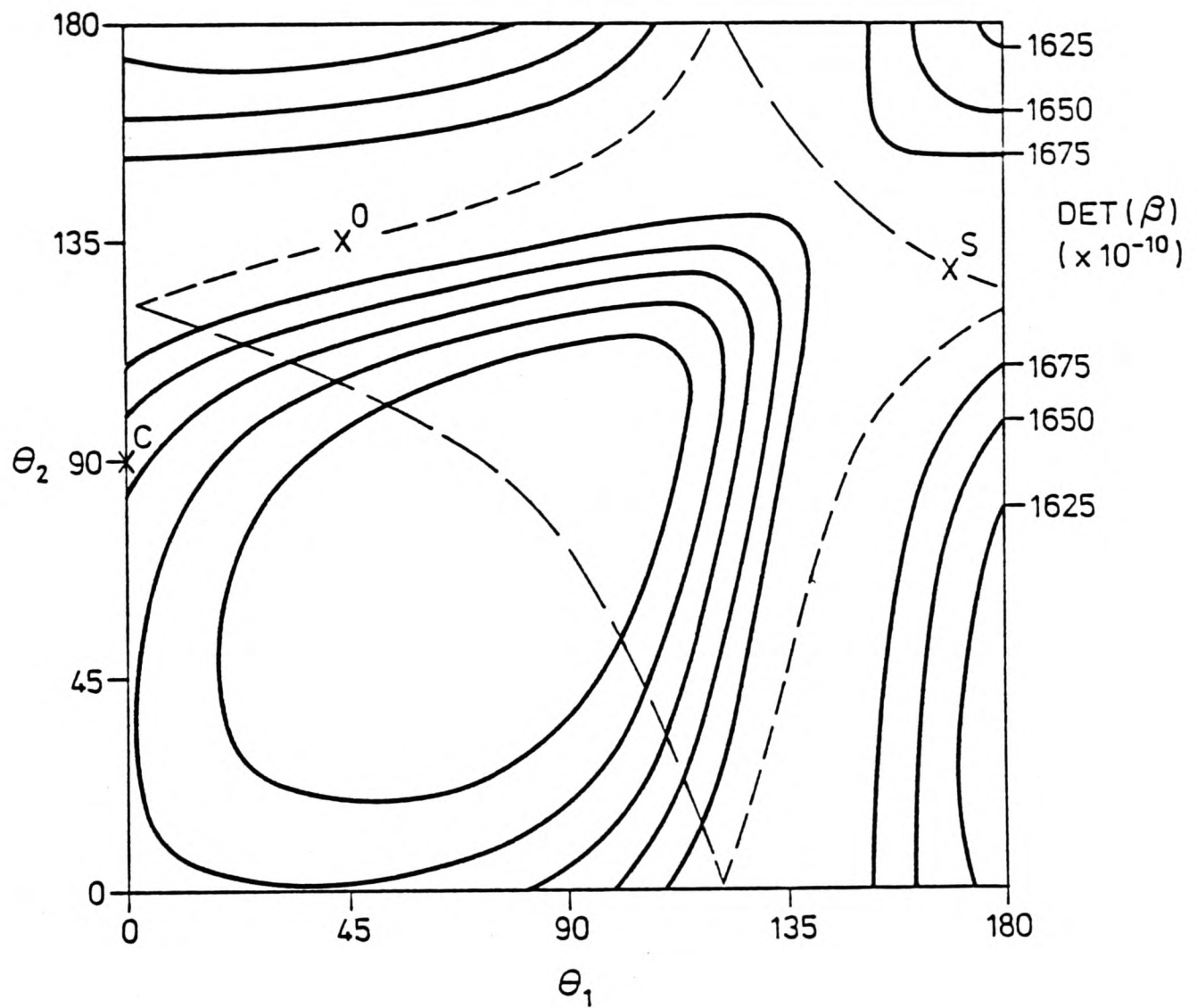


Figure 2 : Contours for  $\text{DET}(\beta)$  (divided by  $10^{10}$ ) for various linear indices of the traits defined by angles  $\theta_1$  and  $\theta_2$  with  $\beta$  estimated by offspring-parent regression. Classes of designs and individual designs are denoted as in Figure 1.

(divided by  $10^{10}$ ) of 233, 235 and 136 in Figure 1 and 1702, 1719 and 1635 in Figure 2 respectively. The ratio  $1702/233 = ((2+ix)/i^2)^3 = 1.94^3$  shows the advantage of using offspring-parent regression with orthogonal designs.

When two linear indices are used to select parents, methods to improve the precision of parameter estimates using offspring-parent regression have been demonstrated, by choosing the linear indices in an efficient way (viz. pairs of orthogonal indices on the canonical scale). An alternative selection criteria on which to select individuals is now considered.

#### ELLIPTICAL SELECTION EXPERIMENTAL DESIGN

When using offspring-parent regression to estimate genetic parameters, the variance of the genetic parameters depends on the sum of squares of the observations on the parents. When only one trait is of interest, the sum of squares is maximised by selecting individuals with high and low values of the trait to be parents (i.e. selection of individuals with extreme values). By analogy, in the two dimensional case, this suggests selecting a proportion  $p_E$  (if the same experimental resources are used as in the divergent selection schemes, then  $p_E$  equals  $2p$ ) of the  $2M$  individuals measured which are as far from the origin as possible. Invariance arguments suggest using a quadratic index of the form  $(x_{1j} \ x_{2j})'P^{-1}(x_{1j} \ x_{2j})$  for the  $j^{\text{th}}$  individual. Geometrically, this can be thought of as selecting individuals outside an ellipse given by the formula  $(x_1+x_2)^2/2(1+r_p) + (x_1-x_2)^2/2(1-r_p) = w^2$ , where  $w$  is chosen such that a proportion  $p_E$  of the individuals are outside the ellipse and,

because this depends on P, the ellipse is called a phenotypic selection ellipse.

Tallis (1963) considered this type of selection in a different context and showed that the proportion  $p_E$  and the variance-covariance matrix of the observations after elliptical selection,  $P^*$ , can be derived as  $p_E = F_2(w^2)$  and  $P^* = [F_4(w^2)/F_2(w^2)] P$  where  $F_k(w^2)$  is the probability that a  $\chi^2$  variable with k d.f. is greater than  $w^2$ . The recursive procedure of Hill and Pike (1966) gives the relationship between  $F_2(w^2)$  and  $F_4(w^2)$ , viz.  $F_4(w^2) = F_2(w^2) + (w^2/2) \exp(-w^2/2)$ , where  $F_2(w^2) = \exp(-w^2/2) = p_E$ . Therefore  $P^* = (1 - \log p_E)P$ .

As before, transformation onto the canonical scale results in the diagonalisation of the F matrix and  $\text{DET}(\beta_C)$  can be written as

$$\text{DET}(\beta_C) = (2Mp_E)^3 d_1 d_2 (d_1 + d_2) (1 - \log p_E)^3 \quad (15)$$

The ratio of the determinants from elliptical selection and the orthogonal index design is  $(2(1 - \log p_E)/(2 + ix))^3 > 1.0$ . For example, when  $p_E$  equals 0.2 and 0.4, the ratio equals  $(1.23)^3$  and  $(1.21)^3$  respectively, which shows the advantage of using the phenotypic selection ellipse rather than selecting on orthogonal canonical indices. Obviously, if no phenotypic selection is performed then  $p_E = 1.0$  and  $p = 0.5$  and the ratio of the two determinants is one.

The selection criteria  $(x_1 \ x_2)' P^{-1} (x_1 \ x_2) = w^2$  can be thought as  $(x_1 + x_2)^2 / 2(1 + r_p) + (x_1 - x_2)^2 / 2(1 - r_p) = w^2$  and  $x_1 + x_2$ ,  $x_1 - x_2$  are the axes of the ellipse. For canonical traits the selection ellipse reduces to a canonical circle which is generated by the orthogonal axes  $C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $C_2 \cos \theta_{C1} - C_1 \sin \theta_{C1}$ , for all values of  $\theta_{C1}$ . These axes are precisely those of the orthogonal

indices suggested in the previous section. This naturally leads to the question if a canonical ellipse generated by the symmetric axes  $C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $C_1 \sin \theta_{C1} - C_2 \cos \theta_{C1}$  can give a more efficient design. The calculation of the sums of squares and crossproducts for the parental values is more difficult and requires numerical integration, (see Appendix 2 for calculation of  $\text{DET}(\beta_C)$ ). The maximum value of  $\text{DET}(\beta_C)$  occurred when the canonical ellipse was rotated by an angle  $\phi$  with values  $0^\circ$  and  $90^\circ$ , for  $0^\circ < \phi < 180^\circ$ . When  $\phi = 90^\circ$ , this corresponds to reparameterising  $C_1$  as  $C_2$  and vice versa. Therefore, the canonical ellipse generated by the symmetric axes gives the most efficient design.

Again there is the difficulty that these axes require estimates of  $G$  and an analytic formula for the optimal angle could not be found. The ratio of values of  $\text{DET}(\beta_C)$  from using the optimal symmetric and orthogonal axes depends on the proportion of individuals selected as parents. For combinations of canonical heritabilities in the range of 0.1 to 0.9 and a range of selection proportions ( $0.05 < p_E < 0.30$ ), the maximum value of the ratio was 1.01. The ratio decreased as the selection proportion increased and as the magnitude of the difference between  $\lambda_1(1-\lambda_1)$  and  $\lambda_2(1-\lambda_2)$  decreased. Therefore, there is a negligible loss of efficiency when using the phenotypic elliptical selection scheme compared with using the optimal elliptical scheme.

Figure 3 shows  $\text{DET}(\beta)$  using ellipses generated by axes  $I_1 = x_1 \cos \theta_1 + x_2 \sin \theta_1$  and  $I_2 = x_1 \cos \theta_2 + x_2 \sin \theta_2$  using the same  $G$  and  $P$  matrices and experimental facilities as in Figures 1 and 2. The values (divided by  $10^{10}$ ) of  $\text{DET}(\beta)$  for the orthogonal (0),

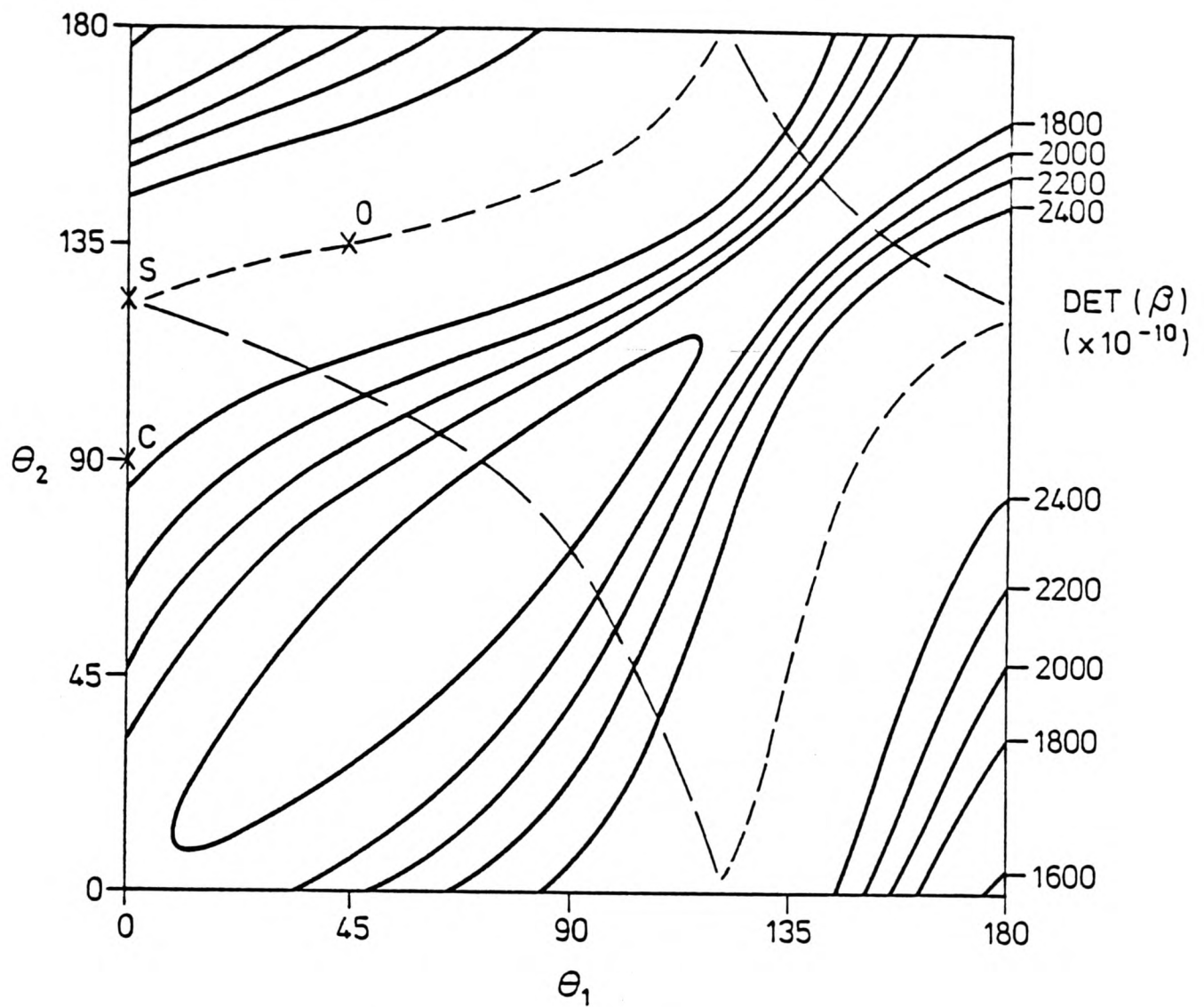


Figure 3 : Contours for  $DET(\beta)$  (divided by  $10^{10}$ ) for various quadratic indices of the traits defined by angles  $\theta_1$  and  $\theta_2$  with  $\beta$  estimated by offspring-parent regression. Classes of designs and individual designs are denoted as in Figure 1.

symmetric (S) and classical (C) axes are 2650, 2652 and 2454 respectively, showing a marked increase over the corresponding values in Figure 2, with  $2650/1702 = (2(1-\log p_E)/(2+ix))^3 = (1.16)^3$ , for the phenotypic selection ellipse.

OPTIMISING THE SELECTION PROPORTION, THE FAMILY SIZE AND  
THE RATIO OF INDIVIDUALS MEASURED IN THE TWO GENERATIONS

If the canonical heritabilities are equal, say to  $\lambda$ , the optimum proportion to select for maximising  $DET(\beta)$  with different estimation methods and selection designs can be found. For example, if  $\beta$  is estimated by response/selection differential the optimal  $p$  is found by differentiation of equation 6 with respect to  $p$ . The solution is given by

$$\frac{(1-r_{OO}\lambda)}{R\lambda(r_{OO}-r_{Op}^2\lambda)} = \frac{2x-i}{4(i-x)p}$$

which suggests that  $p$  must be at least 0.27, that is when  $2x > i$ .

When estimating genetic parameters using offspring-parent regression, the optimal proportion  $p$  is obtained by differentiating equation 12 with respect to  $p$ , which satisfies

$$\frac{(1-r_{OO}\lambda)}{R\lambda(r_{OO}-r_{Op}^2\lambda)} = \frac{1+x^2}{2p(1+ix-x^2)} = W(2,p) \quad (16)$$

which is similar to that of Hill and Thompson (1977), derived in a univariate context,

$$\frac{(1-r_{OO}\lambda)}{R\lambda(r_{OO}-r_{Op}^2\lambda)} = \frac{x^2}{2p(1+ix-x^2)} = W(1,p)$$

The minimum value of the right hand side of  $W(2,p)$  is one when  $p = 0.5$ , and all individuals are then used as parents. When using a phenotypic selection ellipse, differentiating equation 15 with

respect to  $p_E$ , gives the result

$$\frac{(1-r_{00}\lambda)}{R\lambda(r_{00}-r_{op}^2\lambda)} = \frac{-\log p_E}{p_E} = W(3,p_E) \quad (17)$$

These equations give an optimal design for fixed numbers of individuals in the parental,  $2M$ , and offspring,  $2MR$ , generations. If the balance of individuals in the two generations can be adjusted,  $R$ , then the optimal value of  $DET(\beta_C)/(2M(1+R))^3$ , a measure of the efficiency of the design on a per individual measured basis, can be determined. When divergent selection lines are used, the optimum value of  $p$  satisfies

$$\frac{(1-r_{00}\lambda)}{\lambda(r_{00}-r_{op}^2\lambda)} = \left[ \frac{1+x^2}{1+ix-x^2} \right]^2 \frac{1}{2p} = W(4,p)$$

and  $R = (1+x^2)/(1+ix-x^2)$ . When the phenotypic selection ellipse is used, the optimum value of  $p_E$  satisfies

$$\frac{(1-r_{00}\lambda)}{\lambda(r_{00}-r_{op}^2\lambda)} = (\log p_E)^2/p_E = W(5,p_E) \quad (18)$$

and  $R = -\log p_E$ . Figure 4 has been constructed to aid in the solution of the above equations, giving values of  $W(s,q)$  against the total proportion selected,  $p_T$ , where  $q = p_T/2$  for  $s = 1,2$  and  $4$  and  $q = p_T$  for  $s = 3$  and  $5$ .

Since the genetic parameters are not known "a priori", designs should be robust to poor estimates of these parameters. The  $DET(\beta_C)$  values using elliptical selection were calculated for a range of equal canonical heritabilities, with fixed values of  $R$ , at fixed and optimum values of  $p_E$  and were then compared with  $DET(\beta_C)$  values when both the  $p_E$  and  $R$  are optimised (Figure 5). The efficiency of designs when both  $p_E$  and  $R$  are optimised are shown as

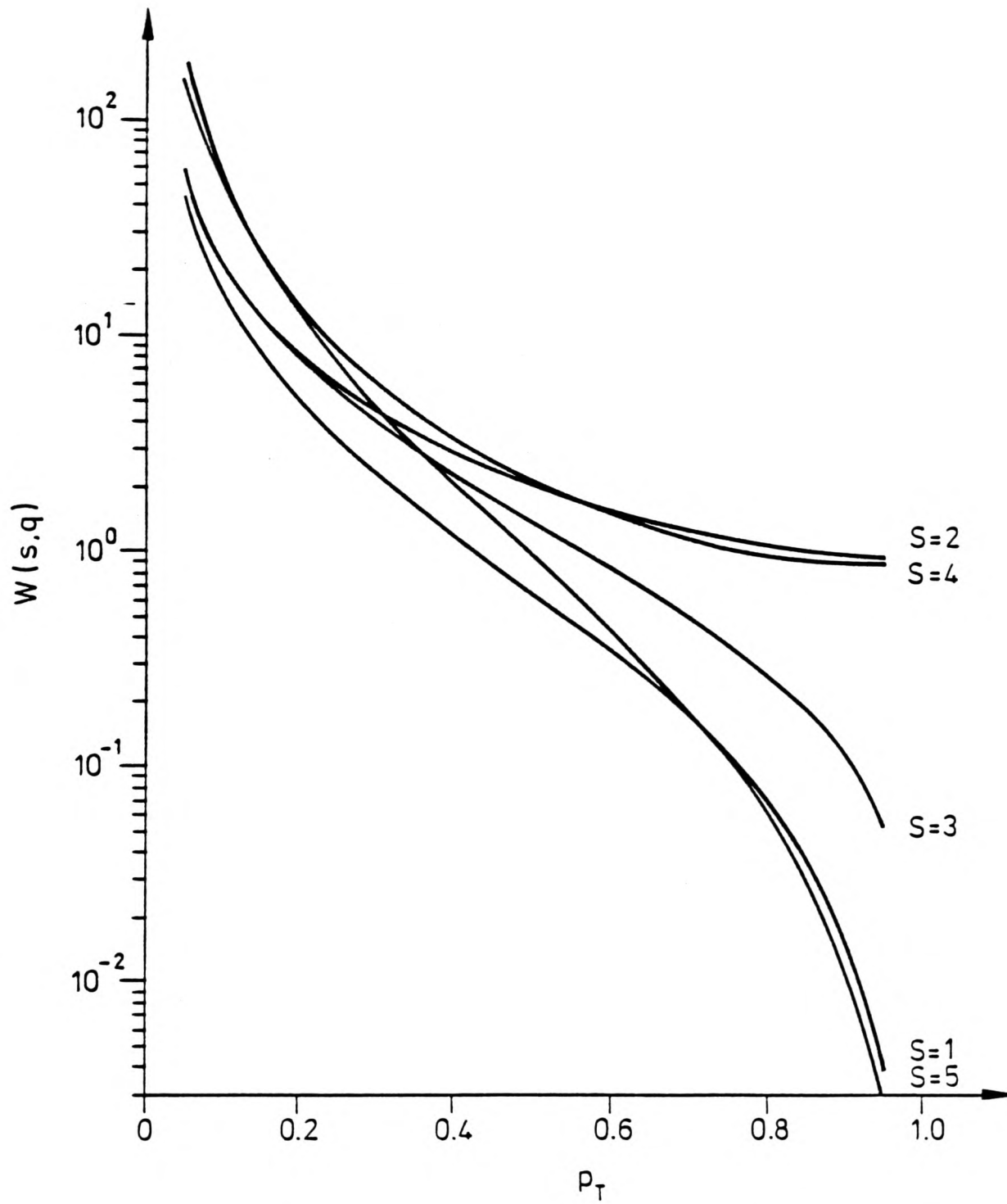


Figure 4 : Values of  $W(s,q)$  plotted against the total proportion selected,  $p_T$ .



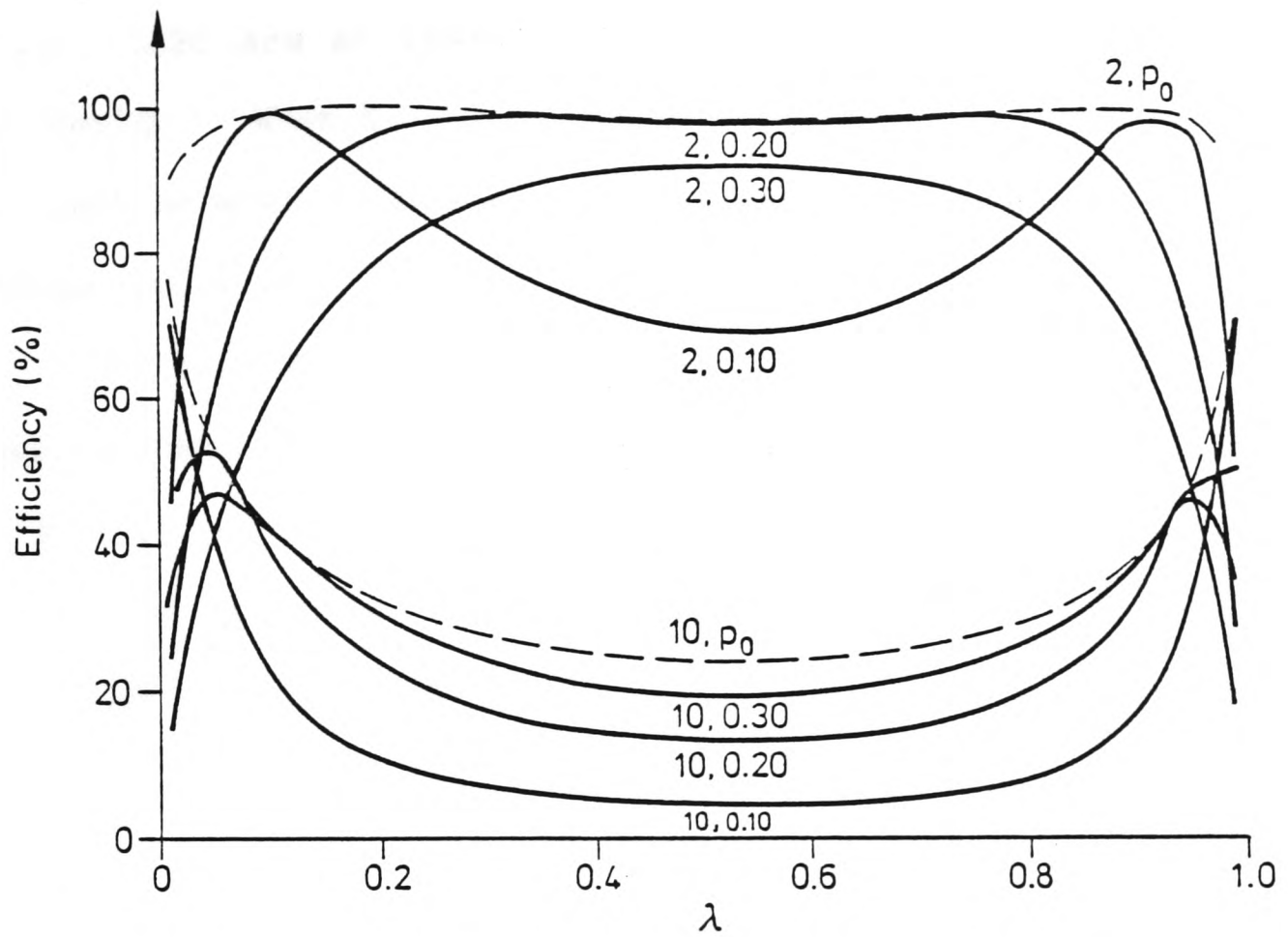


Figure 5 : Efficiency of alternative elliptical designs expressed as  $DET(\beta)$  for a fixed total number recorded relative to that when both  $p_E$  and  $R$  are optimised. Results are given for specified  $R$  and  $p_E$ , with  $p_E$  fixed or optimal ( $p_0$ ).

100 and  $DET(\beta_C)$  values of other designs are shown relative to this base. Figure 5 indicates that for a wide range of canonical heritabilities, with  $R = 2$ ,  $p_E = 0.20$  is efficient. For example, with  $\lambda$  values in the ranges (0.18, 0.87) and (0.13, 0.90) designs using  $p_E = 0.20$  are at least 0.95 and 0.90 as efficient as the optimal design. When  $R = 10$ , designs are generally less than 0.40 as efficient as when  $R$  is optimised, although  $p_E = 0.30$  is close to the optimal value of  $p$ , for  $R = 10$ .

The optimum proportion of individuals to select as parents has been determined, but only when the canonical heritabilities are equal. When the canonical heritabilities are unequal, one suggestion is to use a pooled value of  $\lambda$  in equations 16 to 18, with  $\lambda$  chosen such that the resulting  $d$  satisfies

$$2d^3 = d_1d_2 (d_1+d_2) \quad (19)$$

As there are two solutions to the quadratic equation for  $\lambda$ , it is suggested to use the  $\lambda$  value that lies between  $\lambda_1$  and  $\lambda_2$ . Due to some symmetry in the  $d$  value (i.e.  $\lambda(1-\lambda)$ ), the value of  $\lambda$  is less than 0.5 when  $\lambda_1 + \lambda_2 < 1$  and  $\lambda$  is greater than 0.5 otherwise. The value of  $\lambda$  satisfying equation 19 is essentially independent of the value of  $n$ , the number of progeny per parent, when  $n$  is moderate ( $>15$ ). When no "a priori" estimates of the genetic parameters are available,  $n = 25$  seems a reasonable value to estimate  $\lambda$  with. The values of  $DET(\beta)$  calculated with the optimum  $p_E$  were regressed on the  $DET(\beta)$  values calculated using  $p_E$  derived from equation 17, for combinations of canonical heritabilities in the range 0.1 to 0.9 with various  $R$  and  $n$  values. If the methods of choosing  $p_E$  were identical, then the pooled regression coefficient

and intercept are expected to have values 1.0 and 0.0 and the actual values were 0.980 and 0.003 respectively. Therefore, the use of equation 19 to generate a pooled  $\lambda$  value seems reasonable, for estimation of the optimum selection proportion,  $p_E$ .

#### EXTENSIONS

The gains from using assortative mating when selection is practiced on both male and female parents in one dimensional problems have been demonstrated (Reeve, 1955; Hill and Thompson 1977). The same results apply directly to multivariate designs with selection of mates being based on minimising the "phenotypic distance" between mates.

Selection over several generations can also be effective in increasing the precision. However, the distribution of the progeny measurements, the next parental generation, would not be normal which introduces further complications in the estimation of the variance of the parameters.

Estimation of genetic parameters with a selection ellipsoid is not just limited to two traits. For  $v$  ( $>2$ ) traits the phenotypic selection ellipsoid and transformation onto the canonical scale can be used as before. When the traits have equal canonical heritabilities, the determinant of the inverse of the variance-covariance matrix of the genetic parameter estimates, on the canonical scale, can be written as

$$\text{DET}(\beta_C) = (vMp_E d [F_{v+2}(w^2)/F_v(w^2)])^{v(v+1)/2} 2^{v(v-1)/2}.$$

The optimum proportion of individuals to select can be determined by differentiating  $vMp_E d F_{v+2}(w^2)/F_v(w^2) = vMp_E dK$  with respect to  $p_E$

in order to maximise the value of  $\text{DET}(\beta_C)$ , where  $K = F_{v+2}(w^2)/F_v(w^2)$ . However by defining the function  $W(p_E)$ , the optimal proportion is determined by solving

$$\frac{(1-r_{00}\lambda)}{R\lambda(r_{00}-r_{op}^2\lambda)} = \frac{-1}{p_E} \left[ \frac{K}{p_E \partial K / \partial p_E} + 1 \right] = W(p_E)$$

where  $vMp_E$  is the total number of individuals selected for the ellipsoidal design. The mean parental sums of squares decreases as the number of traits increases and obviously as the proportion selected decreases. However marked gains for increasing the precision of estimates of genetic parameters can be made with at least 5 traits.

#### AN EXAMPLE

An example of a design using elliptical selection is taken from an ABRO sheep experiment to estimate genetic parameters for growth rate and carcass leanness in lambs slaughtered at fixed age. A total of 100 rams are measured and 750 progeny are expected, giving a R value of 7.5. The "a priori" estimates of the heritabilities are 0.20 and 0.40 and the genetic and phenotypic correlations are 0.25 and 0.15 respectively. The canonical traits are  $1.010x_1 - 0.203x_2$  and  $0.052x_1 + 0.991x_2$ , which are phenotypically uncorrelated and have phenotypic variance of 1.0. The canonical heritabilities are 0.192 (derived from  $1.010^2h_1^2 + 2(1.010)(-0.203)r_A h_1 h_2 + (-0.203)^2 h_2^2$ ) and 0.401, and using  $n = 25$  to estimate  $\lambda$ , the value of 0.262 is derived from equation 19. Given the R value of 7.5, the optimum proportion of rams to select,  $p_E$ , is 0.378 from solving  $W(3, p_E) = (-\log p_E)/p_E = 2.57$

(equation 17) or using Figure 4, and so each selected ram has an expected 20 progeny. Therefore 38 rams are selected such that  $x_1^2 + 2(-0.15)x_1x_2 + x_2^2 > 1.94(1 - 0.15^2)$  where  $x_j$  are the standardised measurements of growth rate and carcass leanness. The value of  $w^2 = 1.94$  is derived from  $p_E = \exp(-w^2/2)$ .

The matrix  $X'V^{-1}X_C$  on the canonical scale can be derived using equations 5 and 12 and is diagonal with elements 866, 1578 and 712 using  $d_1 = 11.58$  and  $d_2 = 9.52$  with  $B_1 = B_2 = 38(1 - \log 0.38)$  and  $B_3 = 0$ . Appendix 1 derives the matrix  $R^*$  such that  $R^*\beta = \beta_C$ , and in this case

$$R^* = \begin{bmatrix} 0.102 & -0.411 & 0.041 \\ 0.053 & 0.990 & -0.202 \\ -0.003 & 0.104 & 0.982 \end{bmatrix}$$

The variance-covariance matrix of the genetic parameter estimates is then

$$4(R^*)^{-1}(X'V^{-1}X_C)^{-1}((R^*)^{-1})' = 4 \text{ var}(\beta) = \begin{bmatrix} 46.4 & 7.8 & 1.3 \\ 7.8 & 26.0 & 8.7 \\ 1.3 & 8.7 & 56.0 \end{bmatrix} \times 10^{-4}$$

The expected standard errors for the heritabilities of 0.20 and 0.40 are 0.068 and 0.075 respectively and for the genetic covariance of 0.064 the standard error is 0.051.

If the rams were split into two groups and selected high and low in each group, using an orthogonal design, then the variances of the genetic parameter estimates are proportionately increased by 1.21 (derived from  $2(1 - \log p_E)/(2 + ix)$ ) compared to using elliptical selection. If only information on the parental selection traits is used, then the proportional increase is larger,

1.75 from  $2(1-\log p_E)/(1+ix)$ .

If the classical design is used to estimate the genetic parameters, then the matrix  $X'V^{-1}X$ , determined from equations 9 and 10, equals

$$\begin{bmatrix} 743 & -187 & 11 \\ -187 & 1381 & -175 \\ 11 & -175 & 616 \end{bmatrix}$$

using  $D_{11} = 11.85$ ,  $D_{22} = 9.83$  and  $D_{12} = D_{21} = -1.88$  with

$$\sum_{j=1}^{38} x_{1j}^2 = \sum_{j=1}^{38} x_{2j}^2 = 19(1+ix) + 19(1+ix(0.15)^2) = 62.36 \text{ and } \sum_{j=1}^{38} x_{1j}x_{2j} = 12.84$$

Then  $\sum_{j=1}^{38} s_{1j}^2 = \sum_{j=1}^{38} s_{2j}^2 = 62.7$  and  $\sum_{j=1}^{38} s_{1j}s_{2j} = -5.83$  from equation 11. The

variance-covariance matrix of the genetic parameters is then  $4 \text{ var}(\beta)$ , as before, and equals

$$\begin{bmatrix} 55.8 & 7.7 & 1.2 \\ 7.7 & 31.1 & 8.7 \\ 1.2 & 8.7 & 67.4 \end{bmatrix} \times 10^{-4}$$

Therefore, the proportional increase in the variances of the genetic parameter estimates using the classical design compared to the elliptical design is 1.20.

Note that the matrix of weights on the original scale contributing to the selection indices (B) can be determined from the matrix of weights on the canonical scale ( $ANG_C$ ). If selection is on the orthogonal canonical indices  $I_1 = C_1 + C_2$  and  $I_2 = C_1 - C_2$ , such that  $\theta_1 = 45^\circ$  and  $\theta_2 = 135^\circ$ , then

$$ANG_C = \begin{bmatrix} \cos\theta_{C1} & \sin\theta_{C1} \\ \cos\theta_{C2} & \sin\theta_{C2} \end{bmatrix} = \begin{bmatrix} 0.707 & 0.707 \\ -0.707 & 0.707 \end{bmatrix}$$

and

$$B = \text{ANG}_C S^* = \begin{bmatrix} 0.751 & 0.557 \\ -0.677 & 0.844 \end{bmatrix}$$

Equivalent indices are

$$\begin{bmatrix} \cos\theta_1 & \sin\theta_1 \\ \cos\theta_2 & \sin\theta_2 \end{bmatrix} = \begin{bmatrix} 0.803 & 0.596 \\ -0.626 & 0.780 \end{bmatrix}$$

and the angles of the indices on the original scale are  $36.6^\circ$  and  $128.8^\circ$ .

## SUMMARY

The precision of estimates of genetic variances and covariances obtained from multivariate selection experiments of various designs are discussed. The efficiencies of experimental designs are compared using criteria based on a confidence region of the estimated genetic parameters, with estimation using both responses and selection differentials and offspring-parent regression. A good selection criteria is shown to be to select individuals as parents using an index of the sums of squares and crossproducts of the phenotypic measurements. Formulae are given for the optimum selection proportion when the relative numbers of individuals in the parent and progeny generations are fixed or variable. Although the optimum depends on "a priori" knowledge of the genetic parameters to be estimated, the designs are very robust to poor estimates. For bivariate uncorrelated data, the variance of the estimated genetic parameters can be reduced by approximately 0.4 relative to designs of a more conventional nature when half of the individuals are selected on one trait and half on the other trait. There are larger reductions in variances if the traits are correlated.



APPENDIX 1

The value of  $\text{DET}(\beta)$  can be determined from  $\text{DET}(\beta_C)$ . Since  $G_C = S^*GS^{*'}$ , then

$$\beta_C = 0.5 \begin{bmatrix} G_{C11} \\ G_{C12} \\ G_{C22} \end{bmatrix} = \begin{bmatrix} S_{11}^{*2} & 2S_{11}^*S_{12}^* & S_{12}^{*2} \\ S_{11}^*S_{21}^* & S_{11}^*S_{22}^* + S_{21}^*S_{12}^* & S_{12}^*S_{22}^* \\ S_{21}^{*2} & 2S_{21}^*S_{22}^* & S_{22}^{*2} \end{bmatrix} \beta$$

Let the above 3x3 matrix be denoted  $R^*$ , then

$$\beta_C = R^* \beta \quad \text{and} \quad \beta = (R^*)^{-1} \beta_C$$

$$\text{var}(\beta) = (R^*)^{-1} \text{var}(\beta_C) ((R^*)^{-1})'$$

$$\text{var}(\beta)^{-1} = R^* \text{var}(\beta_C)^{-1} R^{*'}$$

$$|X'V^{-1}X| = |R^*|^2 |X'V^{-1}X_C|$$

As  $S^*PS^{*'} = I$ , then  $|S^*|^{-2} = |P| = (1-r_p^2)$

The determinant of  $R^*$  can be shown to equal  $|S^*|^3$ , therefore

$$\text{DET}(\beta) = (1-r_p^2)^{-3} \text{DET}(\beta_C)$$

APPENDIX 2

In this appendix the calculation of  $p_E$  and the mean sums of squares and crossproducts after elliptical truncation selection is illustrated. The selection ellipse based on symmetric axes is  $C_1 \cos \theta + C_2 \sin \theta$  and  $C_1 \cos \theta - C_2 \sin \theta$  is  $a^2 C_1 + b^2 C_2 = w^2$ , where  $C_1, C_2$  are the canonical variates and  $a^2 = 2 \cos^2 \theta$ ,  $b^2 = 2 \sin^2 \theta$ . Given the proportion to be selected,  $p_E$ , the "size" of the ellipse,  $w$ , satisfies

$$p_E = 1 - \frac{4}{\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} \exp(-C_1^2/2) \int_0^{C_2(C_1)} \frac{1}{\sqrt{2\pi}} \exp(-C_2^2/2) dC_2 dC_1$$

where  $C_2(C_1) = \sqrt{(w^2 - a^2 C_1^2)/b^2}$ . Likewise the mean sum of squares

and crossproducts of the canonical variates after elliptical selection are given by  $SS_1(\theta)$ ,  $SS_2(\theta)$  and  $CP(\theta)$

$$p_{ESS_1}(\theta_1) = 4 \left[ \frac{1}{\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} C_1^2 \exp(-C_1^2/2) \int_{C_2(C_1)}^{\infty} \frac{1}{\sqrt{2\pi}} \exp(-C_2^2/2) dC_2 dC_1 + \frac{1}{\sqrt{2\pi}} \int_{aw^2}^{\infty} C_1^2 \exp(-C_1^2/2) 0.5 dC_1 \right]$$

with  $SS_2(\theta_1) = SS_1(90^\circ - \theta_1)$  and by symmetry  $CP(\theta) = 0$ .

By integrating by parts,

$$p_{ESS_1}(\theta_1) = 4 \left[ \frac{1}{2} \frac{\sqrt{aw^2}}{\int_0^{\sqrt{aw^2}} C_1^2 \exp(-C_1^2/2) p_2 dC_1 + xz + p_1} \right] \quad (A1)$$

$$\text{where } p_1 = \frac{1}{2\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} \exp(-C_1^2/2) dC_1 \text{ and}$$

$$p_2 = \frac{1}{\sqrt{2\pi}} \int_{C_2(C_1)}^{\infty} \exp(-C_2^2/2) dC_2$$

and  $z$  is the height of the ordinate at truncation point  $x$ . If the indices of the selection ellipse are defined by angles  $\theta_{C_1}$  and  $\theta_{C_2}$ , the ellipse can be written as:

$$w^2 = (C_1 \cos \theta_{C_1} + C_2 \sin \theta_{C_1})^2 + (C_1 \cos \theta_{C_2} + C_2 \sin \theta_{C_2})^2$$

$$\text{or } w^2 = 2u^2 \cos^2((\theta_{C_1} - \theta_{C_2})/2) + 2v^2 \sin^2((\theta_{C_1} - \theta_{C_2})/2)$$

where  $u = C_1 \cos((\theta_{C_1} + \theta_{C_2})/2) + C_2 \sin((\theta_{C_1} + \theta_{C_2})/2)$

$$v = C_1 \cos((\theta_{C_1} + \theta_{C_2} + 180^\circ)/2) + C_2 \sin((\theta_{C_1} + \theta_{C_2} + 180^\circ)/2)$$

which is the equation of an ellipse on a scale with orthogonal axes  $u$  and  $v$ . The sums of squares of  $u$  and  $v$  ( $SS_u$  and  $SS_v$ ) can therefore be calculated using equation A1. By transforming back to the canonical scale, the mean sums of squares and crossproducts of

the canonical variates are

$$SS_1 = SS_u \cos^2((\theta_{C1} + \theta_{C2})/2) + SS_v \sin^2((\theta_{C1} + \theta_{C2})/2)$$

$$SS_2 = SS_u \sin^2((\theta_{C1} + \theta_{C2})/2) + SS_v \cos^2((\theta_{C1} + \theta_{C2})/2)$$

$$CP = (SS_u - SS_v)(\sin(\theta_{C1} + \theta_{C2}))/2$$

## CHAPTER 6

### GENETIC RELATIONSHIPS BETWEEN GROWTH AND FOOD INTAKE IN PERFORMANCE TESTED RAM LAMBS : AN INVESTIGATION OF GENETIC VARIANCE COMPONENT ESTIMATION PROCEDURES

#### INTRODUCTION

The main current selection objective in terminal sire breeds of sheep is lamb growth rate (Meat and Livestock Commission, 1985), although future requirements appear to be for efficient lean growth, as with pigs and cattle. The genetic relationships between growth rate, food intake and food conversion ratio need to be quantified, so that calculation of selection indices for growth rate and carcass lean content can take account of correlated changes in food intake. For example, selection programmes in pigs, which have a relatively higher economic weighting on food conversion ratio and carcass lean content than on growth rate, have shown a correlated decline in food intake (Mitchell, Smith, Makower and Bird, 1982). This study estimated the genetic relationships between growth and food intake in performance tested ram lambs. The genetic variances and covariances were estimated using analysis of variance and maximum likelihood procedures. Each of the variance component estimation procedures made use of the performance test and pedigree information in different ways. The estimates of the genetic relationships between performance traits for the various estimation procedures were compared.

## MATERIAL AND METHODS

Between 1978 and 1986, Texel-Oxford ram lambs were performance tested from six weeks of age, with individual weights and food intakes recorded weekly. The Texel-Oxford line was derived from several generations of interbreeding of a Texel-Oxford cross. The rams were born and reared at the Research Station's farm, Blythbank, Tweeddale. Early weaning with a minimum weight of 10kg was achieved by feeding a whole barley and fish meal pelleted supplement. After weaning, the rams were individually penned and fed ad-libitum until the end of test. The number of rams performance tested each year and used in the analysis are given in Table 6.1. Rams with a disease history or with little growth over a three week period were excluded from the analysis. The ages at start and end of performance test changed in 1984 due to experimental requirements of the Institute. Data on growth and food intake from 8 to 16 weeks of age was used in the analysis.

### Statistical analysis

The traits of interest were 8 week (8WT) and 16 week (16WT) weight, food intake on test (FI), average daily gain (ADG) and food conversion ratio (FCR). A multivariate analysis of the five traits would not satisfy the assumptions of a linear mixed model (additivity of fixed and random effects, independence of variance and mean, normality), particularly as some traits are functions of others (e.g.  $FCR=FI/WTG$  and  $ADG=WTG/56.0$  where  $WTG = 16WT-8WT$ ). However, the data might be transformed to better satisfy these assumptions. The effect of power transformations on the data was

TABLE 6.1

## Number of performance tested ram lambs each year

Year	Number of lambs tested	Period of test (weeks)	Number of sire families	Number of sires with performance data	Number of lambs with sire performance data
1978	14	6-16	5	0	0
1979	46	6-16	8	2	3
1980	17	6-16	3	0	0
1981	21	6-16	10	1	3
1982	36	6-16	8	6	27
1983	45	6-16	11	10	43
1984	48	8-20	8	5	27
1985	47	8-20	8	7	42
1986	67	8-20	10	8	53
Overall	341		71	39	198

examined using methodology suggested by Solomon (1985).

A power transformation  $y = (x^\lambda - 1)/\lambda$  for  $\lambda \neq 0$  and  $y = \log x$  for  $\lambda = 0$  was used for each trait with the approximate log likelihood equal to  $-0.5(N-s) \log(\sigma_{e_\lambda}^2) - 0.5s \log(\sigma_{e_\lambda}^2 + k\sigma_{s_\lambda}^2) + \log J(\lambda; x) + \text{constant}$ ; where  $\sigma_{e_\lambda}^2$  and  $\sigma_{s_\lambda}^2$  were the residual and sire variance components of the transformed data respectively;  $N$  and  $s$  were the total number of progeny and sires respectively;  $k$  was the weighted number of progeny per sire and  $J(\lambda; y) = \prod |\partial y_{ij} / \partial x_{ij}|$  was the Jacobian of the transformation and the product was taken over all observations. Variance components were calculated using Henderson Method 3 (Henderson, 1953). A range of  $\lambda$  values was used to identify the transformation which maximised the log likelihood.

An approximate log likelihood for bivariate data, with  $y_1 = (x_1^{\lambda_1} - 1)/\lambda_1$  and  $y_2 = (x_2^{\lambda_2} - 1)/\lambda_2$ , equaled  $-0.5(N-s) \log(\det(\underline{\sigma}_{e_\lambda}^2)) - 0.5s \log(\det(\underline{\sigma}_{e_\lambda}^2 + k\underline{\sigma}_{s_\lambda}^2)) + \log J(\lambda_1; x_1) + \log J(\lambda_2; x_2) + \text{constant}$ ; where  $\underline{\sigma}_{e_\lambda}^2$  and  $\underline{\sigma}_{s_\lambda}^2$  were the matrices of residual and sire variances and covariances of the transformed data respectively. Maximisation of the log likelihood for bivariate data incorporated the variance and covariance information between the traits rather than only the variance information as in the univariate case. Variances and covariances of the transformed data were calculated using Henderson Method 3. The transformations of ADG and FI which maximised the log likelihood for the bivariate case were identified by calculating the bivariate log likelihood of the two variates  $ADG_{\lambda_1}$  and  $FI_{\lambda_2}$  for different values of  $\lambda_1$  and  $\lambda_2$ .

### Variance component estimation procedures

After the appropriate transformations were identified for the traits, the genetic variances and covariances were estimated using different models and procedures : (1) covariance among half sibs (sire model) using Henderson Method 3; (2) sire model (SM) using restricted maximum likelihood (REML; Thompson, 1982); (3) offspring-parent regression and (4) SM with offspring-parent regression using REML. The REML procedure enabled the offspring-parent regression coefficient and the sire variance component to be estimated simultaneously. A property of Henderson Method 3 in variance component estimation is unbiasedness but negative variance component estimates are possible. A criticism of Henderson Method 3 is that the sums of squares are calculated under a fixed model but the expected sums of squares are derived under a mixed model. Hartley and Rao (1967) proposed the maximum likelihood (ML) method for variance component estimation. The ML estimates are non-negative and the procedure does not account for the loss in degrees of freedom from estimation of fixed effects in the mixed model. REML, a modification of ML, takes account of the degrees of freedom needed for estimating fixed effects in variance component estimation. In the sire model, parental performance information is not used in genetic variance estimation. Similarly, the variance between sibs and the variance between family means are not used in the estimation of genetic variances with offspring-parent regression. The sire model with offspring-parent regression gives two estimates of the heritability of the trait but the sire variance component is under-estimated by  $0.25G'P^{-1}G$ , where G and P are the



genetic and phenotypic variance-covariance matrices respectively. In the univariate case the sire variance is under-estimated by  $0.25h^4\sigma_p^2$ .

In each of the above procedures, the only genetic relationships between individuals used in the analyses were those between sire and offspring and sires were assumed to be unrelated. From 1978 to 1982, the performance tested rams were selected for breeding on growth rate (see Chapter 3) and from 1985 the rams were selected for carcass leanness based on an index of ultrasonic backfat and weight at 20 weeks of age. The ultrasonic backfat depths were measured from 1985. The selection over several generations introduces bias to the variance components at two levels. The genetic variance changes with selection (Bulmer, 1971) and variance component estimation procedures such as Henderson Method 3 are biased by selection (Robertson, 1977).

To take account of selection and the generation structure of the data a further three models were fitted using REML (5) SM including sire pedigree information, (6) individual animal model using REML (IAM; Quass and Pollak, 1980) including sire pedigree information and (7) IAM including sire and dam pedigree information.

In each variance component estimation procedure, the fixed effects included in the model were year of birth, age of dam at lambing, birth type (single, twin or triplet) and date of lambing. The variance component estimation procedures were all multivariate analyses except the sire model with offspring-parent regression which was a univariate analysis. The variance component and fixed effect estimates from the univariate sire model with offspring-

parent regression are expected to be identical to those from the univariate sire model with sire pedigree information included in the analysis.

## RESULTS

The log likelihoods of the transformed data were calculated with  $\lambda$  values equal to -1.0, -0.9, -0.8 ... 1.9 and 2.0 for each trait separately. An estimate of the  $\lambda$  value which maximised the log likelihood was obtained by differentiation of the quadratic function which best described the log likelihood in terms of  $\lambda$  values. The maximum value of the log likelihood was compared with the log likelihood when  $\lambda=1$  for 8WT, 16WT, FI and ADG. The comparison for FCR was made with  $\lambda=0$  (a log transformation). The values of the various log likelihoods are given in Table 6.2. Twice the difference between two log likelihoods for one trait has a  $\chi^2$  distribution with one degree of freedom. Only the log likelihood for ADG was significantly increased by use of the power transformation with  $\lambda$  equal to 1.70. The log transformation for FCR was appropriate and as  $\log(\text{FCR}) = \log(\text{FI}) - \log(\text{16WT} - \text{8WT})$ , then variance components for  $\log(\text{FCR})$  can be estimated from variance and covariance components of 8WT, 16WT and FI.

The bivariate log likelihood of FI and ADG was maximised with the average  $\lambda$  value nearer to unity than the two univariate log likelihoods and there was no significant difference between the maximum bivariate log likelihood and the bivariate log likelihood with  $\lambda_1=\lambda_2=1.0$  (Table 6.2). Twice the difference between two log likelihoods for two traits has a  $\chi^2$  distribution with two degrees of

TABLE 6.2

Log likelihoods for 8 and 16 week weights, food intake on (FI), average daily gain (ADG) and food conversion ratio (FCR) for various  $\lambda$  values

Trait	Mean	r.s.d. <sup>+</sup>	$\lambda_{\max}$	Log likelihood $\lambda=\lambda_{\max}$	$\lambda=1.0(0.0 \text{ for FCR})$	2 (difference between) log likelihoods)
8 week wt. (kg)	21.3	3.3	0.89	-414.8	-415.0	0.5
16 week wt. (kg)	41.5	4.5	1.12	-519.2	-519.4	0.3
FI (kg)	76.0	9.4	1.00	-777.9	-778.1	0.4
ADG (g/day)	360	43	1.70	-300.3	-304.3	8.1
FCR (kg/kg)	3.80	0.44	-0.46	291.3	288.9	4.7
FI, ADG			0.78, 1.44	369.6	367.0	5.2

+ Residual standard deviation after fitting fixed effects.

freedom. Variance components for  $ADG = (16WT-8WT)/56$  can be estimated from variance and covariance components of 8WT and 16WT. The subsequent multivariate variance component estimation procedures used data on 8WT, 16WT and FI, as variance components for ADG and  $\log(FCR)$  could be derived from those of 8WT, 16WT and FI.

Estimation of fixed effects is required in the estimation of breeding values in selection programmes. The fixed effect estimates for food intake from six of the estimation procedures are given in Table 6.3 for comparison. There was some variation in the magnitude of the fixed effect estimates between procedures, but the ranking of estimates was similar within procedures. The estimates of fixed effects and their standard errors from the univariate SM with offspring-parent regression were the same as those from the univariate SM with sire pedigree information included in the analysis. Standard errors of fixed effects decreased as the information used in the estimation procedure increased (Table 6.3). For example, the standard errors from Henderson Method 3 were almost twice as large as the standard errors from the individual animal model with sire and dam pedigree information included in the analysis. Food intake on test increased with dam age and decreased with birth type, which reflected the relationship between FI and WTG.

Sire model procedures estimate the sire variance component which includes a quarter of the additive genetic variance. The individual animal model procedures used are intended to estimate the additive genetic variance assuming no maternal effects. In Table 6.4, the sire variance component and residual variance estimates are

TABLE 6.3

Fixed effect estimates for food intake during test for six  
of the estimation procedures (mean = 76.0kg)

Fixed effect	Henderson method 3	Estimation procedure					s.e.d.*	number of lambs
		SM	SM with O-P regression	SM (sire pedigree)+	IAM (sire pedigree)++	IAM (sire and dam pedigree)\$		
Dam age								
1	0.0	0.0	0.0	0.0	0.0	0.0	43	
2	5.5	6.1	5.9	5.0	5.9	6.3	104	
3	7.4	9.5	8.5	7.8	8.5	8.8	88	
4	7.7	9.3	8.6	6.2	8.9	9.6	50	
5	9.3	6.2	9.3	7.5	9.5	10.2	21	
>5	3.0	5.2	3.5	3.7	3.3	4.0	35	
Birth type								
1	0.0	0.0	0.0	0.0	0.0	0.0	108	
2	-4.9	-4.8	-5.2	-5.8	-5.1	-5.9	218	
3	-9.2	-8.5	-9.2	-9.8	-9.1	-10.0	15	
s.e. #	1.85	1.61	1.70	1.62	1.12	1.00		

+ Sire model including sire pedigree information

++ Individual animal model including sire pedigree information

\$ Individual animal model including sire and dam information

‡ Standard error of difference from IAM with sire and dam pedigree

# Ratio of s.e.d. : s.e.d. of IAM (sire and dam pedigree)

TABLE 6.4

Estimates of sire variance ( $\sigma_s^2$ ) and environmental variance ( $\sigma_e^2$ ) components for six of the estimation procedures

Trait	Estimation procedure					
	Henderson method 3	SM	O-P regression	SM with pedigree)+	IAM (sire pedigree)++	IAM (sire and dam pedigree)\$
8 week weight						
$\sigma_s^2$	1.44	1.42	1.48	1.42	0.73	1.07
$\sigma_{s2}$	9.38	9.44	9.44	9.50	10.00	9.87
$\sigma_e^2/\sigma_s^2$	6.51	6.64	6.37	6.67	13.68	9.23
16 week weight						
$\sigma_s^2$	2.22	2.68	2.50	2.57	3.03	3.07
$\sigma_{s2}$	17.91	17.53	17.56	17.69	17.80	17.89
$\sigma_e^2/\sigma_s^2$	8.08	6.53	7.02	6.88	5.88	5.82
Food intake						
$\sigma_s^2$	12.83	13.50	10.66	13.53	14.04	16.34
$\sigma_{s2}$	77.96	77.67	78.26	78.13	79.18	78.65
$\sigma_e^2/\sigma_s^2$	6.08	5.75	7.34	5.78	5.64	4.81

+ Sire model including sire pedigree information

++ Individual animal model including sire pedigree information

\$ Individual animal model including sire and dam pedigree information

given for both the sire and individual animal model procedures. The sire and residual variance estimates increased as more pedigree information was included in the analysis, while the ratio of error to sire variance decreased.

An objective assessment of variance component estimation procedure is the empirical standard deviation of the variance components estimated from replicated simulations of data (Sorensen and Kennedy, 1984). With experimental data, the standard error of the heritability estimate is an obvious criterion for comparing the precision, but not the bias, of the estimation procedures. The heritability estimates and their standard errors for performance traits estimated by seven procedures are given in Table 6.5. The standard error of the regression coefficient for the offspring-parent regression procedure used the between sire about the regression mean square rather than the residual mean square. The precision of Henderson Method 3 and sire model using REML procedures with or without sire pedigree information were similar. The precision of the three estimation procedures which used sire and/or dam pedigree information increased as the pedigree information increased. Hill and Nicholas (1974) showed a positive correlation between the heritability estimates calculated by offspring-parent regression and by covariance of half sibs from the same data set. Conclusions as to the amount of similarity between heritability estimates obtained by different procedures should take account of the correlation structure of the estimates. However, calculation of the appropriate correlation structure is outwith the scope of this chapter.

TABLE 6.5

Heritability estimates for performance traits from seven estimation procedures

Trait	Henderson method 3	Estimation procedure					LAM (sire and dam pedigree)\$
		SM	O-P regression	SM and O-P regression	SM (sire pedigree)+	LAM (sire pedigree)++	
8 week weight							
$h^2$	0.53	0.52	-0.12	-0.04*	0.54#	0.52	0.39
s.e.	0.24	0.22	0.15	0.20	0.23	0.23	0.12
16 week weight							
$h^2$	0.44	0.53	0.14	0.34	0.50	0.51	0.59
s.e.	0.23	0.22	0.20	0.24	0.22	0.23	0.13
Food intake							
$h^2$	0.56	0.59	0.41	0.47	0.48	0.59	0.69
s.e.	0.25	0.23	0.17	0.23	0.22	0.24	0.13

+ Sire model including sire pedigree information

++ Individual animal model including sire pedigree information

\$ Individual animal model including sire and dam pedigree information

\* Estimate from offspring-parent regression

# Estimate from variance components



Log (food conversion ratio) can be adequately expressed as a function of 8WT, 16WT and FI, just as ADG was a function of 8WT and 16WT. The sire and residual variance components for ADG and log (FCR) were derived from variance components of 8WT, 16WT and FI from the multivariate IAM analysis including sire and dam pedigree information, using the equation  $\text{var}(f(x,y,z))=d'Vd$ , where V is the variance-covariance matrix of x, y and z and

$d' = [\partial f(x,y,z)/\partial x \quad \partial f(x,y,z)/\partial y \quad \partial f(x,y,z)/\partial z]$  and  $f(x,y,z)$  is the function of x,y and z whose variance is to be estimated. For comparison, the sire and residual variances were also estimated from the univariate IAM including sire and dam pedigree information. The variance components for log (FCR) estimated from the two methods were in reasonable agreement as the sire and residual variances from the univariate IAM analysis were  $2.78 \times 10^{-3}$  (s.e.  $3.24 \times 10^{-3}$ ) and  $10.32 \times 10^{-3}$  (s.e.  $2.84 \times 10^{-3}$ ) respectively, while the derived sire and residual variances were  $2.43 \times 10^{-3}$  and  $9.80 \times 10^{-3}$  respectively. The corresponding heritability estimates were 0.21 (s.e. 0.24) and 0.20.

Although the sire and residual variances for log (FCR) were adequately derived from variances and covariances of 8WT, 16WT and FI, the genetic relationships between log (FCR) with 8WT, 16WT and FI are more precisely estimated from the multivariate IAM for 8WT, 16WT, FI and log (FCR) with sire and dam pedigree information. Likewise, the genetic relationships between ADG with 8WT, 16WT, FI, and log (FCR) were estimated from analyses including 8WT, FI, log (FCR) with ADG and 16WT, FI, log (FCR) with ADG. When two estimates of a genetic covariance were available (e.g.  $\text{cov}(FI, \log(\text{FCR}))$ ), the estimate from the multivariate analysis of 8WT, 16WT, FI and log

(FCR) was used. The heritability, genetic and phenotypic correlation estimates are given in Table 6.6. The heritability estimates for weight at fixed age were higher than the heritability for average daily gain. Although the heritability for food intake was high, the heritability of log food conversion ratio was 0.08. The genetic correlations between performance traits were high and those between food intake, log food conversion ratio and average daily gain were not significantly different from one.

#### DISCUSSION

The heritability estimates for weight at fixed age and average daily gain are considerably higher than previously published estimates (Wolf, Smith, King and Nicholson, 1981) for crossbred lambs under field conditions. The use of a high energy and high protein diet fed ad-libitum on performance test would not restrict the rams genetic ability for growth rate and food intake. Crossbred lambs under field conditions were limited by the milking ability of their dam and by the lower nutritional quality of grass compared to the performance test diet. The genetic variation for performance traits in the Texel-Oxford, which is a synthetic breed, may be greater than in a traditional terminal sire breed. These two factors may account for the high heritability estimates for growth traits.

The bias in the heritability estimates of the various procedures cannot be quantified, although some qualification of the direction of the bias can be made. An assumption of the Henderson Method 3 and sire model using REML estimation procedures is that all

TABLE 6.6

Heritability, genetic and phenotypic correlations for performance traits

	Trait				
	8 week eight	16 week weight	Food intake	Average daily gain	Log (food conversion ratio)
8 week weight	0.47+ (0.13)	0.85 (0.02)	0.63 (0.04)	0.25 (0.06)	0.48 (0.04)
16 week weight	0.97 (0.03)	0.63 (0.13)	0.79 (0.02)	0.71 (0.03)	0.13 (0.06)
Food intake	0.73 (0.11)	0.88 (0.05)	0.70 (0.12)	0.61 (0.04)	0.46 (0.04)
Average daily gain	0.94 (0.08)	0.92 (0.07)	0.99 (0.02)	0.30 (0.10)	-0.38 (0.05)
Log (food conversion ratio)	0.65 (0.34)	0.81 (0.29)	0.95 (0.14)	0.97 (0.06)	0.08 (0.06)

+ Estimate of heritabilities (on diagonal) and genetic (below) and phenotypic correlations (above) with standard errors in brackets

sires are unrelated and have undergone no selection. The effect of selection and the subsequent genetic relationship between sires will cause the between sire variance component and heritability estimates to be underestimated. The offspring-parent regression procedure has similar assumptions to the above and has no constraint on the sign of the regression coefficient estimate, such that the heritability estimates can be negative. The regression coefficient (b) is a biased estimate of  $0.5h^2$  as  $b = 0.5h^2 + \sigma_{AoAm}/\sigma_p^2$  where  $\sigma_p^2$  and  $\sigma_{AoAm}$  are the phenotypic variance and genetic covariance between dam maternal effects with additive genetic effects of offspring performance (Willham, 1963). The covariance term could be negligible as all offspring were weaned early and there was no subsequent restriction on performance traits due to individual penning and ad-libitum feeding. The sire model and IAM procedures using REML with sire and/or dam pedigree information can take account of the selection provided the selection criteria was a function of the traits in the analysis (Meyer and Thompson, 1984). Inclusion of ultrasonic backfat depth in the selection criteria in 1985 will have biased the genetic parameter estimates. The magnitude of the bias should be small as the estimated genetic correlation of ultrasonic backfat depth and weight at fixed age is less than 0.6 (Parratt, Burt, Bennett, Clarke, Kirton and Rae, 1987) and selection including ultrasonic backfat depth only occurred in 1985. The genetic variance-covariance matrix is constrained to be positive semi-definite in REML estimation procedures and variance component estimates may have a positive bias. The IAM procedure using REML with sire and dam pedigree information does not take

account of maternal effects and heritability estimates will be negatively biased given positive maternal effects. The bias due to assuming no maternal effects was common to all estimation procedures.

The genetic correlation of food intake with weight at fixed age and with growth rate over a fixed time period suggests that food conversion ratio was relatively constant with a low heritability. Thompson, Parks and Perry (1985) found a similar relationship between food intake and growth rate such that divergent selection for weight at 12 weeks of age resulted in no response for food conversion ratio.

Food conversion ratio may be a useful concept for some purposes, but a study of various transformations of FCR demonstrated that  $\log(\text{FCR})$  may be the appropriate function of FCR from a genetic viewpoint. With highly correlated traits, such as WTG, FI and FCR, it is not obvious what the genetic contribution of each trait is to the others. The linear combination of WTG and FI which accounted for the majority of the genetic variation in FCR was  $\text{FI} = 5.95 \text{ WTG} + \text{constant}$ , from principal component analysis of the genetic variance-covariance matrix of WTG and FI. As FI equals  $\text{FCR} \times \text{WTG}$ , then differentiation of the equation for FI with respect to WTG and evaluation at the mean value of FCR also provided information about WTG and FI at constant FCR. The linear relationship was  $\text{FI} = 3.80 \text{ WTG} + \text{constant}$  and the slope was of similar magnitude to the slope of the equation derived from principal component analysis. The two slopes, one genetic and the other phenotypic, suggest that there was little genetic variation in FCR which was independent of

variation in WTG and FI. The slopes from analyses of log traits were 6.49 and 1.00 respectively, which suggested there was relatively more genetic variation, independent of WTG and FI, in log (FCR) than in FCR.

Important linear combinations of FI, 8WT and 16WT were determined from a canonical variate analysis of the genetic and phenotypic variance-covariance matrices. A variate  $C_1 = 0.18 (FI) + 0.05 (16WT) - 0.09 (8WT)$ , with a canonical heritability of 0.69, represented the linear combination which accounted for 75% of the genetic variation in performance. The first canonical variate was essentially  $2FI+WTG$ . The second canonical variate  $C_2 = -0.17 (FI)+0.45 (16WT)+0.02 (8WT)$  had a canonical heritability of 0.43 and accounted for 0.96 of the remaining genetic variation but was less readily interpreted. The canonical heritability of the  $i^{th}$  canonical variate equals  $\lambda_i/(1+\lambda_i)$  where  $\lambda_i$  is the  $i^{th}$  eigenvalue of  $G-\lambda P$ . The eigenvalues were 2.25, 0.75 and  $9.00 \times 10^{-3}$ , the first two canonical variates accounted for 0.997 of the genetic variation in performance traits. Although the sum of eigenvalues (equal to the trace of  $P^{-1}G$ ) is unbiased, the individual canonical heritabilities are biased (Hill and Thompson, 1978). In particular, the larger canonical heritabilities are biased upwards, the smaller downwards and pairs of equal canonical heritabilities are spread apart (Hayes and Hill, 1980). The canonical variates may give some insight into the biological relationships between the traits and also suggest combinations of traits as selection criteria to improve overall performance.

The main objective of this study was to estimate the

genetic relationships between performance test traits, and not to evaluate variance component estimation procedures using a relatively small data set with unknown genetic variances and covariances. The sire and individual animal models which take account of sire and/or dam genetic relationships were compared with Henderson Method 3 and offspring-parent regression procedures for estimating variance components. The former procedures were more precise.

## SUMMARY

Genetic relationships between growth and food intake were estimated from data on 341 performance tested Texel-Oxford ram lambs. During the test period, 8 to 16 weeks of age, all rams were individually penned and fed ad-libitum. The traits analysed were 8 and 16 week weights, food intake on test, average daily gain and food conversion ratio (FCR). Examination of the data, taking account of the sire and residual variances, suggested a log transformation of FCR was appropriate to satisfy the assumptions of a linear mixed model. No transformation of the other traits was required. The heritability estimates for weight at fixed age (0.47, s.e. 0.13 at 8 weeks and 0.63, s.e. 0.13 at 16 weeks) and average daily gain (0.30, s.e. 0.10) were higher than those of crossbred lambs, presumably due to the high energy/protein diet and the lack of maternal effects. The heritability of food intake (0.70, s.e. 0.12) was higher than the heritability of log FCR (0.08, s.e. 0.06). The genetic correlations between growth traits were greater than 0.90 and those between food intake, log FCR and average daily gain were not significantly different from one. A canonical variate analysis of the genetic and phenotypic variance-covariance matrices indicated that the first canonical variate, 2\*food intake + weight gain, accounted for the majority of the genetic variation in performance traits. The sire and individual animal models which take account of sire and dam pedigree information were compared with Henderson Method 3 and offspring-parent regression procedures for estimating variance components. The former methods were more precise.



## CHAPTER 7

### GENERAL DISCUSSION AND CONCLUSIONS

Various questions were posed in the introduction, some of which have been answered and methods to obtain answers to other questions have been suggested. It has been established that improvement in the efficiency of lean meat production in sheep can be achieved through between breed selection followed by within breed selection.

A comparison of performance traits in crossbred progeny of various terminal sire breeds suggested that the ranking of terminal sire breeds for growth and carcass traits was similar to the ranking for mature weight. Therefore, changes in the production system could be met by changing the terminal sire breed in accordance with their mature weight. An exception to the rule was the Texel, which produced leaner carcasses than expected.

Although lamb growth rate can be measured directly, genetic improvement within breeds in growth rate is difficult due to its low heritability and so alternative indirect selection criteria have been studied. Croston *et al* (1981) selected on ram 18-month weight, as adult weight tends to be more heritable than juvenile weight. However, the gains from indirect selection were offset by the increase in generation interval. Selection on lamb growth rate with artificial rearing, in order to reduce maternal effects and give a better indication of a ram's breeding value was examined. The genetic correlation between lamb growth rate under natural and under artificial rearing was markedly less than one, which diminished the effectiveness of reducing maternal effects. There

was no advantage in these alternative selection criteria compared to selecting on lamb growth rate directly.

Carcass traits, for example carcass lean proportion, cannot be measured directly and, unlike growth rate, have heritabilities of about 0.4. Several methods of estimating body composition in the live animal were assessed. Phenotypic correlations between carcass lean proportion and ultrasonic measurements were about 0.4 with a repeatability of measurements of 0.7. The use of ultrasonics may have a valuable role in selection programmes to improve lean meat production. New techniques for estimating body composition in the live animal are becoming available due to recent advances in computer technology. A correlation of lamb carcass lean weight with measurements on images from X-ray computed tomography (CT) of 0.79 has been reported (Sehested, 1984). However, the capital and maintenance costs of a CT are too high for an individual or even a group of breeders to finance. Use of the CT may be limited to a research tool for study of physiological processes in the live animal. However, estimation of carcass composition in the live animal for selection programmes will probably be made using ultrasonic measurements, despite their lower precision than CT.

The use of physical traits, such as liveweight and ultrasonic backfat depth, approach direct selection on the carcass trait. In contrast, physiological traits may be measures of the biology of the carcass traits to be improved. The response to selection for triglyceride content of very low density lipoproteins (VLDL) was a decrease in body fat content but not in liveweight of

poultry. (Griffin, Whitehead and Broadbent, 1982). Although, the site of lipogenesis in poultry, the liver, is different from sheep, the adipocyte, plasma VLDL concentrations may reflect fat metabolism on fasting, with higher plasma VLDL concentrations in fat sheep than in lean sheep. However, the VLDL and NEFA (non-esterified fatty acids) concentrations before, during and after fasting showed no relationship with carcass leanness. The study of genetic relationships between physiological traits and carcass traits is an area which requires further research, which in turn may lead to improvement in the efficiency of lean meat production by reducing the rate of lipogenesis or the rate of protein degradation.

The optimal selection criterion which maximises the rate of genetic improvement towards a given selection objective, weights the information from various sources with appropriate functions of the genetic and phenotypic parameters. Precise knowledge of the genetic and phenotypic parameters for growth and carcass traits are required such that the efficiency of various selection criteria can be compared. Bennett and Clarke (1984) and Rae (1984) examined the efficiency of a series of selection criteria which used information from an individual, its half-sibs and its progeny for growth and ultrasonic measurements or carcass measurements. If the genetic and phenotypic parameter estimates are poorly estimated and incorrect, then progeny testing of rams using expensive carcass dissection techniques may be wrongly recommended as the optimal method of estimating a ram's breeding value for a selection objective, when really the use of half-sib ultrasonic information may give essentially the same breeding value estimate. An error of this

magnitude would have important consequences for the success of a breeding programme. Although, Bennett and Clarke (1984) reached similar conclusions to Rae (1984) about progeny testing and half-sib information, Rae (1984) emphasised that "this tentative conclusion is greatly dependent on the accuracy of the genetic parameters used, some of which are subject to large error".

The correlated responses in several traits to selection on the optimal selection criterion for a particular selection objective can be predicted provided accurate genetic and phenotypic parameter estimates are available. The correlated responses for various selection objectives can be examined and restriction in genetic change for particular traits can be recommended, as required. For example, Parratt and Simm (1987) examined the inclusion of a reduction in genetic change in birth weight in the selection objective, due to the negative genetic correlation of birth weight with lamb survival.

For improvement in carcass traits of crossbred progeny slaughtered at fixed weight or fixed age, the traits which may be included in the selection criterion are liveweight and ultrasonic fat and muscle depth measurements of an individual and its half-sibs at a constant age. The optimal combination of measurements in the selection criterion will depend on the appropriate genetic and phenotypic parameters which are currently imprecisely estimated or unknown. The design of multivariate selection experiments was developed from the need for precise estimates of genetic parameters. A three year bivariate selection experiment which used the new design was started in 1985 at the Institute and carcass lean

proportion and growth rate were the traits of interest. Carcass lean proportion was estimated from an index of ultrasonic backfat depth and liveweight at 20 weeks of age. Performance tested rams were selected each year and their crossbred progeny were slaughtered at fixed age or fixed weight and their carcasses dissected. Precise estimates of genetic and phenotypic parameters for growth and carcass traits for both slaughter criteria will then be available.

The inclusion of food intake in the selection objective was recommended by James (1982) unless there was no genetic variation in food intake which was independent of growth rate. The genetic relationships between growth rate and food intake in performance tested ram lambs were estimated and the estimate of the genetic correlation between the two traits was essentially one. On the basis of this result, the inclusion of food intake in the selection objective is not required. The performance tested rams which were individually penned and fed could therefore have been group penned and fed, without any loss in the accuracy of predicted breeding values for the efficiency of lean meat production.

New methods of measuring biological traits present an ever increasing range of selection criteria. Selection lines for various traits would enable the assessment of the new selection criteria for improving the trait of interest. Therefore as correlated responses to selection for carcass lean weight and carcass lean proportion are expected to be different, selection lines for these two traits have been established in Edinburgh. A study of the direct and correlated responses to selection in these lines of sheep will provide valuable information towards improving lean meat production.

Currently, the performance tested rams from the selection lines are fed a high energy/protein diet to increase the accuracy of selection. The identification of lean and fat rams with ultrasonic technology will be more accurate using an intensive performance test, than if the rams were reared naturally. However, other performance test regimes need to be examined to determine the necessity of an intensive performance test to maximise the rate of genetic improvement of lean meat production.

Knowledge of the appropriate genetic relationships between production traits will allow sheep breeders to select the best animals to maximise the rate of genetic improvement. Each breeding programme may have different requirements and may use the information from this research in various ways. The emphasis of this research is in providing information to the sheep industry to enable it to determine the appropriate method of genetic improvement in terminal sire breeds for lean meat production.

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## PUBLICATIONS

Some results from the thesis have been published as follows

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## ESTIMATION OF CARCASS LEANNESS IN YOUNG RAMS

N. D. CAMERON AND C. SMITH

*AFRC Animal Breeding Research Organisation, West Mains Road, Edinburgh EH9 3JQ*

### ABSTRACT

The accuracy of six methods to estimate carcass leanness in young rams was studied in 36 Texel-Oxford rams, measured at 5 months of age. The rams were slaughtered and dissected. Plasma non-esterified fatty acid and very low density lipoprotein concentrations, sampled before, during and after fasting, showed no relationship with carcass leanness. The same was true for food conversion efficiency measured from 6 to 16 weeks of age, and for measurements taken with the Scanogram ultrasonic machine. The Vetscan and Danscanner ultrasonic machines gave repeatable measurements of fat depth (0.41 and 0.46 respectively). The Vetscan was the best predictor of carcass leanness by proportionally reducing the residual mean square by about 0.20, corresponding to a correlation of  $-0.45$  between ultrasonic fat depth and carcass leanness. Inclusion of average daily gain and ultrasonic fat depth in a selection index would allow appreciable improvements in both traits.

### INTRODUCTION

EXCESS FAT PRODUCTION in British sheep carcasses in 1977 was estimated as 25 000 t, about 0.14 of the total carcass weight produced (Kempster, 1979). The Meat Promotion Executive of the Meat and Livestock Commission (MLC) reported that consumers found lamb the least versatile, fattest and most wasteful of meats (Kempster, 1983). Such waste fat production may be reduced by within-breed selection for leanness facilitated by an effective method of estimating body composition in rams before breeding age. Techniques for live-body measurement in sheep have been reviewed recently by Alliston (1983).

The use of different ultrasonic techniques for predicting carcass composition in sheep has been studied previously by several groups, but it is not always clear whether adjustments for lamb age and weight at the time of assessment were made. The Scanogram was evaluated by Pattie, Thompson and Butterfield (1975) and they concluded that it was of little value in predicting carcass lean content, although it did have some value in predicting fat content.

Shelton, Smith and Orts (1977) scanned Rambouillet rams with the Scanogram and found correlations for total fat trim with ultrasonic fat thickness and eye muscle area of 0.47 and 0.45 respectively. Gooden, Beach and Purchas (1980) reported a correlation of 0.76 between ultrasonic measurements and carcass fat content using a modified 'A' mode scanner. The Danscanner and Scanogram were compared for predicting both carcass lean and subcutaneous fat content by Kempster, Arnall, Alliston and Barker (1982). The proportional reduction in the residual m.s. on using the ultrasonic measurements of fat area for the Danscanner and Scanogram were 0.17 and 0.31 for carcass lean (g/kg) (residual m.s. = 1480) and 0.24 and 0.51 for subcutaneous fat (residual m.s. = 990) respectively. The current report provides more information on the Danscanner and Scanogram and evaluates another scanner, the Vetscan (Fischer Ultrasound Ltd, Edinburgh).

The relationship between plasma triglyceride concentrations and body fat content was also studied. In broilers, Griffin, Whitehead and Broadbent (1982) reported a phenotypic correlation of 0.38 between plasma



triglyceride concentration and fat content. Triglyceride content of plasma very low density lipoprotein (VLDL) and low density lipoprotein (LDL) also showed reasonable correlations with fat content. Selection of male broilers on the basis of VLDL and LDL concentrations produced groups with significant differences in body fat content but little difference in body weight. However, the site of lipogenesis in poultry (liver) is different from that in sheep (adipocyte). Appreciating this, it was hoped that in rams, different amounts of body fat may be reflected in differential rates of fat mobilization on fasting, as detected by plasma VLDL concentrations. The VLDL concentration may indirectly be indicative of carcass leanness as carcass lean and fat proportions are highly correlated (Wolf, Smith, King and Nicholson, 1981).

#### MATERIAL AND METHODS

The comparisons were made on 36 Texel-Oxford young rams born in 1983 on the Animal Breeding Research Organisation's (ABRO) experimental farm at Blythbank, Peeblesshire. The Texel-Oxford line was derived at ABRO from three to four generations of interbreeding of a Texel-Oxford cross. The dams of the rams were 1, 2, 3 or 4 years old at lambing with an even distribution over ages. Lambing took place from mid-March to mid-April (average lambing day of year = 92). Nine sires were used, seven 2-year-olds and two 1-year-olds. The rams were artificially reared and housed from birth with individual food intakes and live weights recorded from 6 weeks of age for a period of 10 weeks. They were all slaughtered at the end of August (day 240 of the year).

Ultrasonic measurements were taken using the Vetscan and Danscanner on days 194 and 222 and the Scanogram on day 229. A single experienced operator used each machine. Details of ultrasonic scanning of sheep using the Danscanner and Scanogram are given by Kempster *et al.* (1982). Wool was clipped

from the scanning site and liquid paraffin used to ensure acoustic contact. Scans were taken of the cross-section of the *m. longissimus dorsi* and overlying fat at the 12th rib. Tissue boundaries were identified on the scan photographs and the following measurements taken; fat depth: fat thickness measured over the *m. longissimus dorsi* 3.5 cm (FD3), 6.0 cm (FD6) from the dorsal mid line and at the dorso-lateral corner of the muscle (FDK); fat area: fat area over the *m. longissimus dorsi* 6.0 cm (FA6) from the dorsal mid line and at the dorso-lateral corner of the muscle (FAK); muscle depth: maximum depth of the *m. longissimus dorsi* (MD); muscle area: area of the *m. longissimus dorsi* (MA).

All the above measurements were taken with the Danscanner and Scanogram, while the Vetscan measured the fat depths, FD6 and FDK, and muscle depth. The Danscanner's fat depth and fat area measurements included skin thickness whereas measurements of the Scanogram and Vetscan did not. Kempster *et al.* (1982) reported that Danscanner ultrasonic measurements, both including and excluding skin thickness, had similar residual s.d. when used as predictors of carcass lean content.

For a 6-day plasma sampling period, starting on day 230, the rams were weighed and bled daily. Plasma VLDL and non-esterified fatty acid (NEFA) concentrations were determined from frozen samples at the end of the test period. On days 1 and 2 of sampling, the rams were fed normally, with straw being fed on day 3. The rams were fasted on days 4 and 5 and then fed normally on day 6. Four days after the end of the test, the rams were slaughtered.

The rams were slaughtered at a mean age of 21 weeks and mean live weight of 42.4 kg. Half carcasses were dissected at the East of Scotland College of Agriculture (ESCA). They were cut into eight standard joints using anatomical reference points (Cuthbertson, Harrington and Smith, 1972) and each joint was dissected into lean, subcutaneous fat, intermuscular fat, bone and waste.

The data were standardized by fitting effects of dam age and birth type; live weight and age at time of measurement were fitted as covariates. The repeatability of ultrasonic measurements was calculated as the residual correlation between measurements. The value of individual ultrasonic measurements, food conversion efficiency (g live-weight gain per kg food intake), NEFA and VLDL concentrations in estimating carcass leanness was assessed by the additional reduction in the residual m.s. after fitting the measurement as a covariate. This is equivalent to testing the significance of the regression coefficient of carcass leanness on the measurement.

The rams examined were those remaining after high and low truncation selection for 100-day weight (trait *X*), as required for another experiment. The effect of stabilizing selection (on the remainder) on the correlation of traits *Y* (ultrasonic fat depth) and *Z* (carcass leanness) is noted in the appendix.

## RESULTS

Means and standard deviations of ultrasonic measurements for the Danscanner, Scanogram and Vetscan are given in Table 1. The proportional increase in fat and muscle depths measured was approx. 0.10, from day 194 to day 222, as detected by the Danscanner and Vetscan. The repeatability of Danscanner and Vetscan fat depth measurements were similar, as were measurements of muscle depth. The change in fat and muscle areas measured did not follow a consistent pattern over the same period of time. The repeatability of muscle area and muscle depth were lower than for fat depth measurements.

The reductions in the residual m.s. of carcass leanness after fitting the fixed effects and covariates are given in Table 2. The base residual m.s. of 628 was used to assess the value of the various predictors of carcass leanness. The proportional reduction in the residual m.s. of carcass leanness on including individual ultrasonic measurements in the

TABLE 1  
*Means and standard deviations of fat area (FA), muscle area (MA) and fat depth (FD) as measured by the Danscanner, Scanogram and Vetscan ultrasonic machines and repeatabilities*

	Day of year	Fat area (mm <sup>2</sup> )		Muscle area (mm <sup>2</sup> ) MA	Fat depth (mm)			Muscle depth (mm) MD
		FA6	FAK		FD3	FD6	FDK	
Mean and (s.d.)								
Danscanner†	194	500 (73)	674 (132)	1372 (240)	7.3 (1.4)	7.4 (1.2)	9.2 (1.8)	24.7 (3.2)
	222	525 (51)	630 (88)	1272 (158)	8.1 (1.0)	8.0 (1.3)	10.6 (1.8)	27.7 (2.5)
Scanogram	229	155 (39)	235 (62)	1276 (216)	2.8 (0.6)	3.3 (0.8)	4.1 (0.9)	20.2 (3.3)
Vetscan	194					1.8 (0.8)	1.8 (0.9)	23.0 (3.5)
	222					1.9 (0.8)	1.9 (0.9)	25.6 (2.3)
Repeatability‡								
Danscanner								
within day	222	0.60	0.84	0.71	0.69	0.63	0.39	0.62
between days		0.48	0.40	0.16	0.55	0.39	0.53	0.27
Vetscan								
between days						0.43	0.40	0.28

† Average of two measurements.

‡ Adjusted for fixed effects, lamb weight and age (s.e. = 0.18).

model are given in Table 3. If the residual m.s. was proportionally reduced by less than 0.01, the ultrasonic measurements are not included in the Table. The Scanogram measurements were of little value in indicating carcass leanness, as shown by their absence in Table 3. For the Danscanner, the fat area measurements were better indicators of carcass leanness than were the fat depth and muscle measurements. However, the Vetscan fat depth measurements provided the best estimate of carcass leanness, by reducing the residual m.s. by about 0.20, corresponding to a correlation of  $-0.45$ .

The means and standard deviations of plasma VLDL and NEFA concentrations and cumulative food conversion efficiency over the 10-week period are given in Table 4. The plasma VLDL concentrations rose on fasting but fell back to normal on refeeding. The plasma NEFA concentrations rose

substantially on fasting and were still elevated at slaughter. Cumulative food conversion efficiency was variable in the first 2 weeks of test, but then remained constant for 4 weeks, and gradually declined for the remaining 3 weeks of test. The proportional reduction in the residual m.s. was less than 0.01 when any of these measurements were included in the model, so they were of little value as indicators of carcass leanness.

#### DISCUSSION

For estimation of carcass leanness from measurements on the live animal, the average of the Vetscan fat depth (VFD) measurements gave the best estimate here, reducing the residual m.s. by 0.20. This held for the measurements on two occasions, so the results were repeatable. However, it should be noted that earlier published results with the Scanogram were encouraging (Kempster *et al.*, 1982), but these were not supported in this trial. It is important to confirm the present results of the Vetscan in another set of material. The results may be improved by scanning the rams at heavier weights, as fat depth would be greater and differences may be easier to detect. In practice, the estimation of carcass leanness could be improved by taking several independent measurements on each ram, at two or more locations on two or more occasions.

At present, there is little financial incentive to produce leaner lamb carcasses in the

TABLE 2  
*Reduction in the residual m.s. of carcass leanness (g/kg) after fitting fixed effects with lamb age and weight as covariates*

	Carcass leanness
No. of observations	36
Mean value	553.5
Residual m.s.	1109
Residual m.s.	
Effects included in model	
Fixed effects	758
Fixed effects and lamb age	784
Fixed effects and lamb weight	652
Fixed effects and lamb weight and age	628

TABLE 3  
*Proportional reduction in the residual m.s. for carcass leanness by including ultrasonic measurement in the model†*

	Day	Fat area (mm <sup>2</sup> )		Fat depth (mm)		
		FA6	FAK	FD3	FD6	FDK (FD6 + FDK)/2
Danscanner	194	11‡	0	5	2	0
	222	12‡	15‡	3	12‡	3
Vetscan	194				29‡	13‡
	222				14‡	20‡
						23‡
						18‡

† After fitting fixed effects with lamb age and weight as covariates.

‡ Regression coefficient of carcass leanness with ultrasonic measurement statistically significant from zero ( $P < 0.05$ ).

TABLE 4  
Means and standard deviations of plasma very low density lipoprotein (VLDL) and non-esterified fatty acid (NEFA) and cumulative food conversion efficiency

	Day of test					
	1	2	3	4	5	6
VLDL†	{ 28.7	{ 31.7	{ 35.8	{ 38.4	{ 37.2	{ 28.0
	{ 10.6	{ 12.3	{ 12.7	{ 10.6	{ 10.3	{ 10.1
NEFA†	{ 37.0	{ 30.6	{ 276.0	{ 601.9	{ 658.0	{ 735.3
	{ 27.9	{ 24.4	{ 133.3	{ 183.1	{ 153.3	{ 127.9

	Week of test								
	1	2	3	4	5	6	7	8	9
Cumulative food conversion efficiency‡	{ 217	{ 322	{ 305	{ 303	{ 306	{ 301	{ 285	{ 274	{ 269
	{ 226	{ 87	{ 64	{ 45	{ 35	{ 37	{ 33	{ 31	{ 28

† Plasma VLDL and NEFA concentrations measured in mmol/l × 100.

‡ Cumulative food conversion efficiency, from 6 to 16 weeks of age, measured in g live-weight gain per kg food intake.

TABLE 5  
Estimated responses from selection on different traits† assuming equal selection intensities

Response	Selection on a single trait		Selection index to improve		
	ADG‡	VFD§	ADG	Lean	Lean + ADG
ADG	0.10¶	0.02	0.10	0.05	0.08
Lean	0.03	0.13	0.06	0.13	0.12

† Response is expressed in multiples of the phenotypic s.d. and selection intensity *i*.

‡ ADG: average daily gain from birth to slaughter.

§ VFD: Vetscan fat depth.

|| Lean: carcass lean proportion.

¶ Estimates of heritability (on diagonal) and correlations phenotypic (above) and genetic (below).

	ADG	VFD	Lean
ADG	0.10	0.00	0.08
VFD	-0.22	0.12	-0.45
Lean	0.15	-0.58	0.41

United Kingdom, though there is much industry concern about overfatness. Current selection in terminal sire breeds is mainly for growth rate (MLC, 1983). Future requirements in terminal sire breeds seem to be for fast growing leaner animals, as with pigs and cattle. Estimated genetic responses in average daily gain (ADG) and carcass

leanness from selecting directly on each trait and by index selection are given in Table 5. Estimates of the phenotypic and genetic correlations and heritabilities for ADG and carcass lean proportion were obtained from Wolf *et al.* (1981). The genetic correlation of VFD and ADG and carcass leanness were derived from Wolf *et al.* (1981) with adjustments for the ultrasonic measurements. The corresponding phenotypic correlations for VFD used were from the current data. A heritability of ultrasonic fat depth of 0.12 was reported by Bennett, Rae, Clarke and Kirton (1983). Growth rate and leanness were given equal economic weights to form a simple index since it is difficult to derive future economic weights for these traits. With this selection index, appreciable responses can be obtained in both traits. However, derivation of future economic weights for terminal sire breeds is required for calculation of an economic index. On a national scale, even small changes in carcass leanness in nucleus flocks of terminal sire breeds by the use of ultrasonics, would provide substantial benefits to the meat industry, of the order of £0.1 million per annum by reducing the proportion of waste fat produced by 0.01 (Kempster, 1979).

## COMPARISON OF TERMINAL SIRE BREEDS FOR GROWTH AND CARCASS TRAITS IN CROSSBRED LAMBS

N. D. CAMERON AND D. J. DRURY

*AFRC Animal Breeding Research Organisation, West Mains Road, Edinburgh EH9 3JQ*

### ABSTRACT

Performance records for the progeny of matings of Oxford, Texel, Texel-Oxford, Charollais, Charmoise and Meatline rams with crossbred ewes were analysed. The lambs, born from 1980 to 1982, were randomly allocated to three slaughter groups: (1) slaughter at fixed weights of 36 and 38 kg for ewe and castrated lambs; (2) slaughter according to estimated fat cover; (3) slaughter at a fixed age of 4.5 or 5.5 months with half-carcass dissection. The analyses were by least squares and effects were fitted for terminal sire breed, breed of maternal grand sire, year of birth, age of dam at lambing, birth-rearing type and sex of lamb and all two-way interactions. The results followed a well-established pattern where weight for age rankings were constant from birth, through weaning, to slaughter. Progeny of Oxford rams were the heaviest, followed by Texel-Oxford, Meatline and Charollais, Texel and Charmoise in that order. Lambs sired by rams of low mature weight reached a fixed weight at a later age than those sired by rams of high mature weight. They also reached a similar degree of fat cover at an earlier age and at lighter weights than the larger breeds. The carcass traits indicated that Texel crosses had a higher lean and lower fat proportion than would be expected from their growth and mature weight.

The comparative performance of crossbred lambs from 15 terminal sire breeds was assessed, at the same proportion of carcass subcutaneous fat, by combining the results of three experiments.

### INTRODUCTION

INFORMATION ON GROWTH and carcass traits of progeny from different terminal sire breeds is required by producers of commercial lambs to facilitate choices in relation to production system and changes in market requirements. Previous work by the Animal Breeding Research Organisation (ABRO) (Wolf, Smith and Sales, 1980) and the Meat and Livestock Commission (MLC) (Croston, Guy, Jones and Kempster, 1983) compared several terminal sire breeds. This study extended the range of breeds to include two recent imports from France (Charollais and Charmoise) and a synthetic breed (Meatline; Fell, 1979). The other breeds compared were the Texel which has been noted previously for an unusually high lean proportion, the Oxford which is the largest Down breed and the Texel-Oxford cross. The Texel-Oxford line was derived at ABRO from three to four generations of interbreeding of a Texel-Oxford cross.

### MATERIAL AND METHODS

#### *Ewe flock*

Crossbred ewe lambs were produced, from 1979 to 1981, on an Ayrshire hill farm, out of Scottish Blackface ewes mated to rams of several crossing sire breeds (Scottish Blackface, Border Leicester, Oldenburg, Texel, East Friesian, Cambridge, ABRO Damline and Romney). After weaning, the crossbred ewe lambs were transferred to ABRO's lowland experimental farm in Staffordshire.

#### *Terminal sires*

The crossbred ewes were mated at 6 months of age and for 2 subsequent years to Texel, Texel-Oxford, Charollais, Charmoise and Meatline ram lambs. Oxford rams were also used in 1981. The Texel rams were the progeny of imported Dutch and French stock. In each year, there were three or four rams of each breed, although in 1979 and 1980,

nine Texel-Oxford rams were used, making a total 62 rams used during the experiment. Different rams were used each year and were chosen as being representative of the breeds.

Crossbred ewes within each age group and crossbred type were randomly allocated each year to each sire breed, resulting in an average of 19 crossbred ewes per ram, with single-sire paddock matings. Immediately after lambing, mis-mothering was prevented by individually penning ewes and their litters for 12 h, and there was no fostering. Any lamb born outside the range of  $145 \pm 4$  days of its dam's recorded mating date was considered of uncertain pedigree and not included in the analysis.

Records kept for each lamb born were breed of sire and maternal grand sire, identity of sire and dam, date of birth, sex and birth-rearing type. The lambs were weighed at birth and at 4, 8, 12 and 16 weeks of age ( $\pm 3$  days). Weaning took place when lambs were 16 weeks old.

#### *Lamb slaughter groups*

*Fixed age.* Each year, 50 pairs of twin-reared lambs, from 2- or 3-year-old ewes and representing the six terminal sire breeds, were randomly selected for slaughter and dissection at either 4.5 months of age ( $\pm 7$  days) or 5.5 months of age with mean live weights of about 35 and 40 kg respectively.

*Fixed weight.* Half the remaining lambs (with odd-number identities) were slaughtered when reaching a fixed weight of 36 kg for ewe lambs and 38 kg for castrates.

*Fat cover.* The third group of lambs (with even-number identities) were slaughtered at an equal estimated level of fat cover. The level of fat cover was assessed by the condition scoring technique. All carcasses were graded by the MLC. In addition, carcass appraisal data were available for lambs slaughtered at fixed weight or level of fat cover.

#### *Carcass dissection*

Carcass dissections were carried out, each year, on the 50 pairs of twin-reared lambs

slaughtered at fixed ages. The lambs were all slaughtered at one abattoir and MLC carcass classification information (MLC, 1981) and cold carcass weights were recorded for all lambs before being sent for dissection. Half the lambs were dissected by the MLC, Blisworth, and half by the East of Scotland College of Agriculture (ESCA) with the six terminal sire breeds represented equally at both locations. The kidney knob and channel fat (KKCF) was removed and the carcass was cut into eight standard joints using anatomical reference points (Cuthbertson, Harrington and Smith, 1972). Each joint was dissected into lean, subcutaneous fat, intermuscular fat, bone and waste. Information regarding the differences in time and place was available from both within and between twin pairs (litters). The intra-litter correlation coefficient was calculated and the within- and between-litter estimates were weighted accordingly to give an overall estimate of the differences between the two dissection centres and times of slaughter. For slaughter and carcass traits the intra-litter correlation coefficient ranged from 0.21 to 0.26.

#### *Statistical analysis*

Hierarchical least-squares analysis of variance was performed for each trait with progeny nested within dams, which were nested within sires (Harvey, 1960). Effects were fitted for terminal sire breed, breed of maternal grand sire, day and year of birth of lamb, age of dam at lambing, birth type and sex of lamb and all two-way interactions, with effects being tested against the appropriate error mean squares. In the birth weight model, a birth type effect was included. However, as the rearing type of a lamb was not always equal to its birth type, due to mortality of its sibs, a birth-rearing type effect was included in the model for postnatal traits. Birth-rearing categories were (1,1), (2,1), (2,2), (3,1), (3,2) and (3,3), where the first digit refers to birth type and the second to rearing type. Date of birth was included in the analysis of birth weight and carcass traits, as the lambs were slaughtered

on fixed dates. Initially, all terms were included in the models. Effects were then dropped sequentially using the backward elimination technique (Hocking, 1976) until only significant ( $P < 0.10$ ) effects remained. The least-squares constants presented were obtained from the resulting reduced model for each trait. For each comparison of breed constants, the appropriate standard error of the difference was calculated, due to the unbalanced nature of the data, and a  $t$  test performed.

#### RESULTS

There were no statistically significant differences in litter size from birth to 16 weeks between the terminal sire breeds. Although at 16 weeks, the litter size of crossbred ewes mated to Oxford rams was 1.54 compared with the average of the other breeds of 1.72 (s.e. 0.12). It is necessary that there should be no confounding of litter size and sire breed, when the performance of progeny from terminal sire breeds is compared, and therefore, birth-rearing type was included in the model.

##### *Live weights*

The least-squares constants for lamb live weight and rates of weight gain at the various ages are given in Table 1. By 12 and 16 weeks of age, the progeny from Oxford and Texel-Oxford rams were heaviest, those

from Charmoise the lightest, while the Charollais, Meatline and Texel progeny had intermediate weights.

Daily growth rates dropped steadily with age, until 12 weeks when the mean rate decreased from 261 to 150 g/day at 16 weeks. The ranking of the sire breeds for rate of weight gain in each of the 4-weekly periods from birth to 16 weeks followed no consistent pattern, although differences between breeds were evident after 4 weeks of age. However, from birth to 16 weeks, the Charmoise crosses generally grew slower than the others, while the Texel-Oxford and Oxford crosses grew faster.

The ranking of the sire breeds for mean daily weight gain from birth to 16 weeks was the same as for 16-week weight, confirming the close relationship between growth rate and live weight. The ranking of the breeds for mean growth rate and mature live weight was similar ( $r = 0.92$ ; s.e. 0.45), but the Texel crosses had a lower mean growth rate than expected. The estimates of mature weight were obtained from the MLC (1981) and D. Croston (personal communication).

##### *Slaughter at fixed live weight*

The slaughter ages and weights are given in Table 2. At fixed slaughter weight, the lower age of Oxford crosses indicates that they maintained their growth advantage over the other crosses after weaning. Likewise, the

TABLE 1  
*Overall means and least-squares constants for pre-weaning growth traits by sire breed*

	No.	Birth weight (kg)	Live weight at week				Weight gain between weeks				
			4	8 (kg)	12	16	0 to 4	4 to 8	8 to 12 (g/day)	12 to 16	0 to 16
Overall mean	1928	3.85	12.9	21.4	28.7	32.7	318	300	261	150	257
Sire breed†											
Charmoise	258	-0.24a	-1.0a	-1.7a	-1.5a	-1.7a	-23a	-25a	3ab	-8a	-13a
Texel	358	-0.07b	0.3b	0.1b	-0.3b	-0.3b	7b	-12b	-8a	0ab	-2b
Meatline	263	0.00b	0.1b	0.1b	-0.4b	0.0b	5b	-4bc	-5a	10b	0bc
Charollais	271	-0.01b	-0.1b	0.1b	0.0bc	0.2b	1b	13cd	-5a	0ab	1bc
Texel-Oxford	659	0.05b	0.4b	0.5b	0.4c	0.6bc	10b	5cd	-1ab	4ab	4cd
Oxford	119	0.13b	0.3b	0.9b	1.8d	1.2c	-1b	23e	17b	-6ab	10d
Approx. s.e.		0.04	0.12	0.17	0.18	0.20	3	4	4	4	4

† Column values not followed by a common letter differ significantly ( $P < 0.05$ ).

Charmoise crosses had later slaughter dates indicating a slower post-weaning growth rate. The Charollais, Meatline and Texel-Oxford crosses reached slaughter weight about 11 days earlier than the Charmoise crosses and 7 days later than the Oxford crosses, although the latter result was not statistically significant. The initial experimental design provided for ewe and castrated lamb slaughter weights of 36 and 38 kg respectively, but in practice the range of weights was from 30 to 50 kg. In the analysis, the range was restricted to 34 to 40 kg in order to obtain more precise estimates of breed differences with slaughter at fixed weight. The slaughter weights for ewe and castrated lambs in the restricted data set averaged 36.9 and 38.2 kg respectively. There were no differences in carcass weight among the sire breeds. The MLC overall carcass conformation scores for Charmoise and Charollais crosses were one point higher than those for the other breeds. The overall subcutaneous fat cover scores for the Charmoise and Texel crosses were the highest and lowest respectively. The MLC carcass appraisal scheme also records conformation scores for the leg, loin and shoulder joints separately and the residual

correlation coefficients between overall conformation scores and these individual joint scores were 0.88, 0.89 and 0.91 (s.e. 0.04) respectively.

#### *Slaughter at constant level of fat cover*

For lambs slaughtered according to level of fat cover, there were no statistically significant differences in slaughter age, although the Oxford crosses were slaughtered about 6 days earlier than the other crosses and at heavier slaughter weights. The Charmoise crosses had significantly lighter slaughter weights than the other crosses. The ranking of the sire breeds for carcass weight was the same as for slaughter weight with the Oxford and Charmoise crosses having significantly heavier and lighter weights, respectively, than the other crosses. For each breed, the MLC overall carcass conformation scores and subcutaneous fat cover scores were similar for lambs slaughtered according to fixed weight or level of fat cover. The MLC recommend that producers market the majority of lambs with MLC carcass classifications of fat class 2 or 3L and 0.76 of the lambs slaughtered according to fat cover were in these fat classes.

TABLE 2  
*Overall means and least-squares constants for slaughter traits by sire breed*

	Lambs slaughtered according to								
	Fixed weight					Level of fat cover			
	No.	Age (days)	Carcass weight (kg)	Carcass conformation (MLC)	Subcutaneous fat cover (MLC)	Slaughter			Carcass weight (kg)
No.						Age (days)	Weight (kg)		
Overall mean	651	154	16.7	8.4†	8.0‡	993	145	37.5	16.5
Sire breed§									
Charmoise	104	10a	-0.1a	0.7	0.9	128	2a	-2.2a	-0.8a
Texel	125	2ab	0.0a	-0.3	-0.6	188	1a	0.4b	0.2bc
Meatline	93	0b	-0.1a	-0.5	-0.3	131	0a	-0.1b	-0.1b
Charollais	93	-1b	0.1a	0.6	0.2	133	2a	-0.6ab	-0.1b
Texel-Oxford	196	-3b	0.0a	-0.4	-0.4	347	0a	0.8b	0.1bc
Oxford	40	-8b	0.0a	-0.1	0.2	66	-5a	1.7b	0.7c
Approx. s.e.		3	0.17				2	0.31	0.14

† Conformation: 1 = poor; 15 = good.

‡ Subcutaneous (external) fat cover overall: 1 = extremely little fat; 15 = extremely fat.

§ Column values not followed by a common letter differ significantly ( $P < 0.05$ ).



### Carcass dissection

The results are given in Table 3. Breed differences in slaughter weight were similar when lambs were slaughtered at different ages (140 and 170 days) to those when lambs were slaughtered according to body condition at an average of 145 days of age. This suggests that the relative differences between breeds were constant over time and the lack of a statistically significant sire-breed  $\times$  slaughter-time interaction is consistent with this.

Carcass weights of Charollais and Texel-Oxford crosses were significantly heavier than the Charmoise crosses by 1.2 kg, and the other breed crosses were 0.8 kg heavier but not significantly. The Charmoise crosses had significantly higher killing-out proportions than the Texel, Oxford and Texel-Oxford crosses, with the Charollais and Meatline crosses intermediate.

The carcasses of Charmoise crosses had a lower total lean weight than the others by 1.2 kg, on average, and Texel-cross carcasses had lower total fat weight by 1.0 kg, on average. The ranking of the breeds for lean weight was opposite to the ranking for fat weight. Similarly, the proportions of carcass lean and fat had the same rankings as for

total lean and fat weight, respectively, although the breed differences were larger. The Texel crosses had proportionately more lean, 62 g/kg carcass weight, and less fat, 73 g/kg, than the Charmoise crosses, with the Meatline and Charollais crosses intermediate. The Texel crosses had proportionately more lean, 50 g/kg, and less fat, 47 g/kg than the Oxford crosses, while the Texel-Oxford crosses had proportionately more lean, 21 g/kg, and less fat, 19 g/kg, than the Oxford and were similar to the mean of the Texel and Oxford breed crosses. The residual correlation of total lean weight with total fat weight was 0.45 (s.e. 0.06) and that of carcass lean proportion with fat proportion was -0.90 (s.e. 0.06), after fitting fixed effects.

Mean slaughter weights at 4.5 and 5.5 months of age were 38.1 kg and 43.5 kg respectively. Carcasses of the later slaughter time were 1.6 kg heavier and contained proportionately less lean, 12 g/kg carcass weight, more fat, 20 g/kg, and less bone, 8 g/kg. The killing-out proportions at the two slaughter times were the same. The sire-breed  $\times$  slaughter-time interaction was not statistically significant for any trait.

TABLE 3  
Overall means and least-squares constants for carcass traits by sire breed

	No.	Slaughter weight (kg)	Carcass weight (kg)	Killing out (g/kg)	Half-carcass weight			Composition of carcass		
					Lean (kg)	Fat (kg)	Bone (kg)	Lean (g/kg carcass weight)	Fat	Bone
Overall mean	293	40.8	16.8	413	4.6	2.3	1.3	553	276	159
Sire breed†										
Charmoise	50	-2.8a	-0.8a	12a	-0.5a	0.2a	-0.1a	-27a	35a	-10a
Texel	52	-0.6b	-0.2ab	-2b	0.2b	-0.4b	0.0b	35b	-38b	2bc
Meatline	48	0.2b	-0.1ab	-1ab	0.0b	0.0a	0.0bc	-1c	0cd	2bc
Charollais	47	0.5b	0.5b	6ab	0.1b	0.1a	0.0bc	1c	4cd	-5ab
Texel-Oxford	77	1.2b	0.4b	-4b	0.2b	0.0a	0.1c	6c	-10d	3c
Oxford	19	1.6b	0.3ab	-11b	-0.1ab	0.1a	0.1bc	-15ac	9ac	8c
Approx. s.e.		0.50	0.26	3.3	0.07	0.06	0.02	4.0	4.6	1.7
Slaughter time										
4.5 months	149	-2.7	-0.8	0	-0.2	-0.2	0.0	6	-10	4
s.e.		0.22	0.20	2.5	0.03	0.03	0.01	1.7	2.0	0.7
Dissection centre										
ESCA	151		-0.4	-7	-0.33	0.13	0.00	-27	28	4.3
s.e.			0.11	1.5	0.03	0.03	0.01	1.7	1.8	0.7

† Column values not followed by a common letter differ significantly ( $P < 0.05$ ).

Differences between dissection centres were statistically significant for all carcass traits except total bone weight. The ESCA carcasses were, on average, 0.8 kg lighter than the MLC carcasses. This resulted in a difference in killing-out proportion of 14 g/kg. ESCA carcass total lean and fat weights were 0.66 kg lighter and 0.26 kg heavier, respectively, than MLC weights. Thus the ESCA lean proportion was lower, 54 g/kg carcass weight, and the fat proportion was higher, 56 g/kg.

The proportions of total carcass lean found in each of the eight joints are given in Table 4. There were statistically significant differences between sire breeds for all joints except chump and middle neck. However the maximum difference between breeds was 16 g/kg carcass lean for the leg joint. This would result in a maximum difference between breeds of 40 g lean weight for the leg joint, which is unlikely to be economically significant. Sire-breed differences of higher priced joints (leg, chump, loin and best end neck) were also small (9 g/kg). These results show small but statistically significant differences in the lean tissue distribution, of crossbred lambs, due to sire breed, a finding also noted by Wolf (1982). As with carcass

traits, there were small differences between slaughter times and between dissection centres for each joint. There were statistically significant year  $\times$  dissection-centre interactions for all joints except leg, loin and middle neck.

#### DISCUSSION

For all the traits analysed, there was no evidence of a crossing-sire-breed (sire of ewe)  $\times$  terminal-sire-breed interaction. This result agrees with that of Wolf *et al.* (1980) and suggests that, within the range of crossbred-ewe types considered in the experiments, the crossbred-ewe type is of little importance when comparing the performance of progeny from various terminal sire breeds.

As slaughter weight largely determines fat content of the carcass, Bradford (1974) suggested a slaughter weight for crossbred lambs of 0.60 to 0.65 of the mean mature weight of their parental breeds as a commercial guide to standardize carcass composition. However, the proportion of assessed carcass subcutaneous fat is a common alternative slaughter criterion in the current United Kingdom market. Accordingly, the data were adjusted to an equal proportion of dissected subcutaneous fat in

TABLE 4  
*Proportion of carcass lean (g/kg carcass lean) in the different joints by sire breed*

	No.	Leg	Chump	Loin	Breast	Best-end neck	Middle neck	Shoulder	Scrag
Overall mean	293	255	83	100	114	77	120	216	30
Sire breed†									
Charmoise	50	-8a	0a	3a	6a	2a	0a	-4a	0ab
Texel	52	8c	-1a	-4b	-4b	-5b	2a	4b	1ab
Meatline	48	3bc	1a	1ab	-1b	1a	-2a	-2ac	-2b
Charollais	47	0ab	-1a	2a	1ab	1a	-2a	1ab	0ab
Texel-Oxford	77	1b	1a	-4b	0b	-2b	2a	1bc	1a
Oxford	19	-4ab	0a	3ab	-2b	3a	1a	0abc	-1ab
Approx. s.e.		1.6	0.9	1.4	1.3	0.9	1.0	1.1	0.8
Slaughter time									
4.5 months	149	4.0	-0.7	-1.7	-2.3	-0.3	-0.7	0.6	1.7
s.e.		1.2	0.4	0.6	0.6	0.4	0.6	0.5	0.6
Dissection centre									
ESCA	151	-0.6	3.3	-5.0	3.7	-1.8	2.3	-0.4	1.8
s.e.		0.7	0.6	0.6	0.9	0.4	0.5	0.5	0.6

† Column values not followed by a common letter differ significantly ( $P < 0.05$ ).

the carcass using the pooled within-breed regression, there being no evidence of statistically different regression coefficients for the six breeds. The results from this analysis were then combined with those of two other trials (Table 5), using the overlap in breeds among trials, to give information on a total of 15 terminal sire breeds. The least-squares estimates of breeds were obtained from a weighted analysis of variance using the number of observations for each of the breeds means as weights and fitting constants for each trial, in an attempt to minimize the problems created by combining data from different environments and different years.

At the same proportion of carcass subcutaneous fat, slaughter age and carcass weight were positively correlated between sire breeds ( $r = 0.81$ ,  $P < 0.05$ ) which suggests that breeds of heavier mature weight tend to take longer to reach a particular level of subcutaneous fat, which results in heavier carcasses. This is in agreement with the

hypothesis of McClelland and Russel (1972) that if breeds of different mature weight were slaughtered at the same degree of maturity, then the fat proportion would be similar for all breeds. At the same proportion of carcass subcutaneous fat, the correlation coefficients of estimated breed mature weight with slaughter age and carcass weight were 0.84 and 0.72 ( $P < 0.05$ ), respectively. This indicates that the growth rates of crosses from the 15 breeds studied, tend to follow a well-established pattern, where weight for age rankings are reasonably consistent from birth, through weaning, to slaughter.

From these results it may be concluded that a first approximation to the performance of a terminal sire breed may be obtained from a knowledge of its mature weight. Growth rates, slaughter age and weight for a similar level of fat cover could be then estimated. Deviations from these first approximations are expected, such as the Texel in proportions of carcass lean and fat.

Different terminal sire breeds may be suited to different production systems. For example, when the objective is to produce lamb carcasses to a fixed level of fat cover, the larger sire breeds (e.g. Suffolk and Texel-Oxford) would be expected to produce heavier and older lambs than those of the lighter sire breeds (e.g. Southdown and Charmoise). Changes in the production system could be met by changing the terminal sire breed in accordance with their mature weights.

Market requirements for carcass quality and perhaps breed acceptance may also affect the choice of terminal sire breed. For example, substitution of the Suffolk by the Texel may not be economically viable unless the disadvantage of greater slaughter age, due to lower growth rate, is offset by a premium for the production of lean carcasses. Other problems associated with changes in live weight, such as lambing difficulties and subsequent mortality, will also have to be considered. However, the currently important traits of growth rate, carcass weight and level of fat cover can readily be determined by

TABLE 5

*Comparative performance of crossbred lambs from 15 terminal sire breeds at the same proportion of carcass subcutaneous fat (pooled results from three trials)*

Sire breed	Trial†	Mature weight (kg)‡	Carcass weight (kg)	Slaughter age (days)
Southdown	3,.	61	14.0	131
Charmoise	1	62§	15.8	164
Dorset Down	2,3	77	15.3	144
Hampshire Down	3	78	15.4	145
Ile de France	2,3	78	16.2	158
Oldenburg	2	79§	16.3	170
North Country				
Cheviot	3	82	16.6	170
Charollais	1	85§	17.5	162
Meatline	1	85§	17.6	167
Texel	1,2,3	87	17.3	169
Suffolk	2,3	91	17.0	156
Texel-Oxford	1	93	17.7	165
Border Leicester	3	94	17.5	191
Oxford	1,2,3	100	17.2	160
Wensleydale	3	113§	18.3	207

† 1 = Current trial; 2 = Wolf, Smith and Sales (1980); 3 = Croston, Guy, Jones and Kempster (1983).

‡ Mature weights from MLC (1981) except those marked § from D. Croston, MLC (personal communication).

choosing among breeds of terminal sires, on the basis of their mature live weight.

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## RESPONSES IN LAMB PERFORMANCE FROM SELECTION ON SIRE 100-DAY WEIGHT

N. D. CAMERON AND C. SMITH

*AFRC Animal Breeding Research Organisation, West Mains Road, Edinburgh EH9 3JQ*

### ABSTRACT

Forty-one Texel and Texel-Oxford sires were selected over 5 years (1978-82) on high and low adjusted 100-day weight from 174 ram lambs artificially reared from birth and performance tested. The correlated responses to selection were measured in 1103 crossbred progeny, out of an experimental group of crossbred ewes, the progeny being naturally reared in field conditions. Hierarchical analysis of variance was performed, fitting the usual fixed effects and interactions. Co-heritabilities ( $r_A h_1 h_2$ ;  $r_A$  is the genetic correlation between traits with heritabilities  $h_1^2$  and  $h_2^2$ ) were estimated from offspring-parent regression and from the realized responses to selection. The selection differentials achieved (1.70 standard deviations in 100-day weight between high- and low-weight sires) were lower than expected, due to mating difficulties, mortality and other requirements for the stock. The co-heritabilities for growth traits were generally positive but small (mean 0.08; s.e. 0.08). Though not statistically significant, lambs slaughtered at a fixed weight from the high-weight rams were slaughtered earlier with lighter and leaner carcasses, as expected. Similarly, lambs slaughtered according to fat cover from high-weight rams were slaughtered later with heavier slaughter and carcass weights. Generally, the co-heritabilities for carcass traits were not significantly different from zero for either slaughter group. On the basis of these results, selection on ram 100-day weight with artificial rearing may not offer any advantage over natural rearing in the improvement of lamb growth and carcass traits.

### INTRODUCTION

THE main current selection objective in terminal sire breeds of sheep in the United Kingdom is lamb growth rate (Meat and Livestock Commission (MLC), 1983). However, genetic improvement of growth rate in lambs is difficult due to its low heritability with natural rearing (Wolf, Smith, King and Nicholson, 1981). Adult size tends to be more heritable than juvenile size, but Croston, Read, Jones, Steane and Smith (1983) found that selection on 18-month weight was not very effective in the improvement of lamb growth. Owen, Brook, Read, Steane and Hill (1978) selected on ram 90-day weight, with artificial rearing, to remove post-natal maternal effects, and concluded that this was an effective method of selecting rams for improving lamb growth rate. This study estimated the correlated responses in the performance of naturally-reared lambs from crossbred ewes due to

selection on ram 100-day weight with artificial rearing.

### MATERIAL AND METHODS

Between 1978 and 1982, 174 Texel and Texel-Oxford rams were artificially reared and selected on live weight at 100 days of age. The Texel-Oxford line was derived at the Animal Breeding Research Organisation (ABRO) from three to four generations of interbreeding of a Texel-Oxford cross. The rams were born and artificially reared on ABRO's experimental farm at Blythbank, Tweeddale. They received their dam's colostrum and were removed from the dam within 6 h of birth. After 12 to 18 h, the rams were fed half-strength, warm substitute milk, to accustom them to an artificial teat. The milk was gradually increased to full strength, *ad libitum*, over 2 to 3 days. To enable weaning at 6 weeks of age, with a minimum of 10 kg live weight, the rams were

also given pellets of whole barley and fish meal supplement twice daily at 4 weeks of age and once daily at 5 weeks of age. After weaning, the rams were individually penned and fed *ad libitum* until the end of test at 16 weeks of age. At the end of test, the lambs were turned out to grass and the pelleted food was reduced as they became accustomed to the grass. The rams were run with, or grazed alongside, ewes to help develop normal mating behaviour.

Each year, groups of rams were selected for high and low 100-day weight, adjusted for birth type (single or twin born), age of dam, date of birth and age of ram at weighing. For selection purposes, the adjustment factors were calculated from the rams born in each year. Thus, there were different factors in different years. To determine comparable selection differentials for each year, common adjustment factors were used for all rams, using the combined data on 174 rams. Breed-of-ram and year-of-birth effects were also included in the analysis. Five lambs with a disease history or with little growth over a 3-week period were discarded from the selection and the analysis.

The rams were mated at 6 months of age to a flock of crossbred ewes on ABRO's lowland experimental farm in Staffordshire. The flock consisted of crosses out of Scottish Blackface ewes by rams of eight breeds (Scottish Blackface, Border Leicester, Oldenburg, Texel, East Friesian, Cambridge, ABRO Damline and Romney). Ewes within each age group and crossbred type were randomly allocated each year to the rams, resulting in an average of 19 crossbred ewes per ram, with single-sire matings. Mismothering was prevented by individually penning ewes and their litters immediately after lambing, and there was no fostering. The crossbred lambs were reared naturally under normal management practice. Any lamb born outside the range of  $145 \pm 4$  days of its dam's recorded mating date was considered of uncertain pedigree and not included in the analysis. Records kept for each lamb born were breed of sire and maternal grand sire, identity of sire and dam, date of birth, sex and birth-rearing type. The lambs were weighed at birth, 4, 8, 12 and 16

weeks of age ( $\pm 3$  days) and were weaned at 16 weeks of age.

Each year, half of the lambs (with odd-number identities) were slaughtered at a fixed weight of 38 kg for ewe lambs and 40 kg for castrated male lambs. The remaining lambs were slaughtered at an equal estimated level of fat cover. The level of fat cover was assessed by the farm staff using the condition-scoring technique of the MLC (1981). The lambs were all slaughtered at one abattoir, where MLC carcass classification (MLC, 1981), appraisal information and cold carcass weight were recorded.

Hierarchical least-squares analysis of variance was performed for each trait with progeny nested within dams, which were nested within sires. Effects were fitted for terminal sire breed, breed of maternal grand sire, day and year of birth of lamb, age of dam at lambing and sex of lamb and all two-way interactions, with effects being tested against the appropriate mean square. For the birth-weight model, a birth-type effect was included. However, as the rearing type of a lamb was not always equal to its birth type, due to mortality of its sibs, a birth-rearing type effect was included in the model for post-natal traits. For lambs slaughtered at fixed weight, actual slaughter weight was included in the model as a covariate. Initially, all terms were included in the models. Effects were then dropped sequentially using backward elimination (Hocking, 1976) until only significant ( $P < 0.10$ ) effects and interactions remained.

When selection is on trait 1 (sire 100-day weight) for improvement in trait 2 (lamb trait), one of the parameters required for predicting the genetic response through indirect selection can be estimated, namely the co-heritability ( $r_A h_1 h_2$ ) (Yamada, 1968), where  $h_i^2$  is the heritability of trait  $i$  and  $r_A$  is the genetic correlation between the two traits. The co-heritability can be estimated from the offspring-parent regression and, analogous to the realized heritability, from the ratio of the response in the progeny to the selection differential of the parents (Falconer, 1981), with response defined as the difference in mean phenotypic value of progeny from high- and low-weight sires for

trait 2. The most efficient design for estimating co-heritability is offspring-parent regression with selection of high and low groups of parents. However, the difference in efficiency between the two methods from a single generation of selection is small if the co-heritability is low (Hill, 1971). Both methods were used and the results compared.

## RESULTS

The numbers of rams and progeny in the high and low selection groups by year and breed are given in Table 1. The selection differentials achieved each year were reasonably similar (Table 1), except for the small differential in 1981, when another trial had priority in selection. The difference in adjusted 100-day weight between selected high and low rams, weighted by the number of

progeny per ram, was 7.50 kg, corresponding to 1.70 standard deviation (s.d.) units.

Differences in weight between the progeny of the high and low rams were generally positive but quite small (Table 2). The co-heritability estimates, with standard errors from the offspring-parent regression method, were also low and not significantly different from zero. These co-heritability estimates were, on average, proportionally smaller than the estimates from the realized responses, and the standard errors were of similar magnitude. As the rams were artificially reared and their progeny naturally reared, all the estimates are co-heritability estimates rather than heritability estimates.

The results for lamb slaughter and carcass traits, for the two slaughter criteria are given in Table 3. For lambs slaughtered at a fixed weight, the mean slaughter weights were

TABLE 1  
*Numbers and breeds of rams by year and selection type*

Ram year of birth	Ram breed	No. tested	No. selected		Mean 100-day weight (kg)	Selection differential (kg)	No. of progeny	
			High	Low			High	Low
1978	Texel	21	4	4	30.5	6.4	108	122
1979	Texel	16	2	2	36.2	10.0	55	57
	Texel-Oxford	36	5	5	36.9	10.2	131	138
1980	Texel	22	2	2	28.9	8.8	44	25
1981	Texel-Oxford	42	3	1	42.5	2.1	78	25
1982	Texel-Oxford	37	5	6	43.1	6.8	143	132
	Overall	174	21	20	35.5	7.5	559	499

† Overall mean plus least-squares constants, adjusted for birth type and dam age.

TABLE 2  
*Overall means for lamb weight at different ages, the difference between progeny of high and low sires, the offspring-parent regression coefficients and the co-heritability estimates*

Age (weeks)	Mean weight (kg)	Residual s.d. (kg)	Response high-low			Co-heritability†		Regression on sire weight		Co-heritability‡	
			(kg)	s.e.		s.e.	(kg/kg)	s.e.		s.e.	
Birth	4.0	0.65	0.07	0.04	0.05	0.072	0.01	0.005	0.08	0.075	
4	12.6	1.88	0.11	0.12	0.07	0.076	0.01	0.015	0.05	0.071	
8	20.5	2.83	-0.11	0.18	-0.04	0.076	-0.00	0.023	-0.01	0.072	
12	27.5	3.51	0.28	0.23	0.09	0.076	0.03	0.034	0.08	0.087	
16	32.5	3.92	0.26	0.26	0.08	0.078	0.03	0.038	0.08	0.086	

† Derived from response/selection differential.  $\text{Response}_2 = 0.5 (r_{Ah_1h_2})$  selection differential,  $(\sigma_2/\sigma_1)$  where subscripts denote traits: 1 = sire 100-day weight with artificial rearing; 2 = lamb trait with natural rearing;  $\sigma_i$  = phenotypic standard deviation of trait  $i$ .

‡ Derived by setting offspring-parent regression coefficients =  $0.5 (r_{Ah_1h_2}) (\sigma_2/\sigma_1)$ .

TABLE 3

Overall means for progeny slaughter traits with slaughter at fixed weight or level of fat cover, the difference between progeny of high and low sires and the offspring-parent regression coefficients

Trait	Slaughter at fixed weight (no. of lambs = 542)						Slaughter on level of fat cover (no. of lambs = 561)					
	Mean	Residual s.d.	Response high-low	s.e.	Regression on sire weight	s.e.	Mean	Residual s.d.	Response high-low	s.e.	Regression on sire weight	s.e.
Slaughter age (days)	155	26.6	-3.79	2.65	-0.38	0.265	142	29.7	4.17	2.77	0.11	0.418
Slaughter weight (kg)	38.7	2.08					37.2	3.26	0.58	0.30	0.04	0.080
Carcass weight (kg)	17.1	1.55	-0.19	0.15	-0.03	0.012	16.6	2.20	0.35	0.20	0.02	0.042
Killing-out proportion (g/kg)	441	40.7	-4.7	3.9	-0.81	0.34	445	43.9	2.9	4.1	0.05	0.61
Subcutaneous fat score†	7.9	1.71	-0.40	0.16	-0.03	0.022	7.5	2.04	-0.14	0.19	-0.01	0.038
Internal fat score‡	2.3	0.93	-0.24	0.09	-0.02	0.011	2.2	0.95	-0.10	0.09	-0.01	0.011
Conformation score§	8.0	2.27	-0.34	0.17	-0.03	0.021	7.5	1.92	0.17	0.19	0.01	0.27

† Subcutaneous fat score: 1 (low) to 15 (high).

‡ Internal fat score: 1 (low) to 5 (high).

§ Conformation score: 1 (poor) to 15 (good).

TABLE 4

Estimates of co-heritability from offspring-parent regression with slaughter at fixed weight or level of fat cover

	Slaughter at fixed weight		Slaughter on level of fat cover	
	Co- heritability†	s.e.	Co- heritability†	s.e.
Slaughter age (days)	-0.12	0.08	0.03	0.13
Slaughter weight (kg)			0.19	0.34
Carcass weight (kg)	-0.17	0.07	0.10	0.21
Killing-out proportion (g/kg)	-0.17	0.07	0.01	0.13
Subcutaneous fat score	-0.14	0.12	-0.06	0.20
Internal fat score	-0.23	0.11	-0.14	0.11
Conformation score	-0.15	0.10	0.06	0.13

† Co-heritabilities derived from offspring-parent regression estimates.

37.8 kg for ewe lambs and 39.7 kg for castrated male lambs, close to the weights intended in the design of the experiment. The coefficient of variation for slaughter weight was lower for lambs slaughtered at a fixed weight (0.054) than for lambs slaughtered according to fat cover (0.088). The progeny from high 100-day weight rams were slaughtered earlier with lighter and

leaner carcasses, which had significantly lower subcutaneous fat and internal fat scores and poorer conformation scores than lambs from low-weight rams. For lambs slaughtered at a common condition score, none of the differences between progeny groups were significantly different from zero, but progeny from high 100-day weight rams were slaughtered later and at heavier weights, and



the carcass weight and killing-out proportion were also greater. The MLC recommend that producers market the majority of lambs with MLC carcass classifications of fat class 2 or 3L, and the proportion of lambs slaughtered according to fat cover in these fat classes was 0.64.

For the two slaughter criteria, the co-heritabilities for slaughter and carcass traits were generally small and not significantly different from zero (Table 4).

#### DISCUSSION

The co-heritability estimates, although not significantly different from zero, suggest consistent trends in crossbred lamb performance from selection on ram 100-day weight with artificial rearing. The results from the two slaughter groups are different, as expected, showing the importance of defining the response criteria when estimating genetic parameters. Progeny of high 100-day weight rams were slaughtered earlier with lighter and leaner carcasses when slaughtered at a fixed weight, but were slaughtered later with heavier slaughter and carcass weights when slaughtered according to fat cover. Though the practical value of the co-heritability estimates is limited by their large standard errors, they indicate that some genetic progress can be made in lamb performance

from selection on sire 100-day weight with artificial rearing.

The experimental design required 16 pairs of high and low 100-day weight rams (trait 1) with 30 progeny per ram, in order to detect a statistically significant ( $P < 0.05$ ) co-heritability for growth traits of naturally-reared progeny (trait 2), with a 0.80 probability ( $h_1^2 = 0.20$ ,  $h_2^2 = 0.10$ ,  $r_A = 0.90$ ) and a design selection differential of 3.0 s.d. units. This is equivalent to selecting the extreme 0.16 of high- and low-weight rams. In practice, using the adjusted ram-weight data, the maximum selection differential possible would have been 2.4 s.d. units, equivalent to selecting the extreme 0.28 of high- and low-weight rams. However, the selection differential was 1.7 s.d. units, which was essentially equivalent to choosing the high-weight rams at random from rams heavier than the mean weight, and similarly for low-weight rams. Selecting low-weight rams with an equal average deviation from overall mean weight as the high-weight rams proved difficult, as some of the low-weight rams died or failed to mate successfully. These rams were replaced, with the result that the selection differential was reduced. Similar problems were reported by Owen *et al.* (1978).

Performance testing of ram lambs with

TABLE 5  
*Comparison of this study with the second field trial of Owen, Brook, Read, Steane and Hill (1978)*

	Present study		Owen <i>et al.</i>
	Texel-Oxford	Texel	Suffolk
Terminal sire breed			
No. of rams tested	174		86
Proportion (number) selected	0.120 (41)		0.12(20)
Mean weight (kg) (age in days) at selection	36.3 (100)		39.0 (95)
Slaughter weight s.d. (kg)	4.4		4.4
Selection differential (kg)	7.5		12.0
Mean number of progeny per ram	26		28
Mean weight of progeny (kg)	32.5 (27.5)†		33.0‡
Residual s.d. of progeny within sires (kg)	3.9 (3.5)†		4.4‡
Mean square for ram family means	11.6 (5.4)†		43.7‡
d.f.	34 (34)†		9‡
Regression coefficient on ram weight (kg/kg)	0.034 (0.032)†		0.135‡
s.e.	0.038 (0.034)†		0.033‡

† Progeny traits at 112 (84) days of age.

‡ Progeny traits at a combination of 84 and 113 days of age.

artificial rearing has been reported by Broadbent and Watson (1967) and by Owen *et al.* (1978), both using Suffolk rams. No selection was practised by Broadbent and Watson (1967) as only 15 rams were performance tested. Owen *et al.* (1978) reported a co-heritability estimate for lamb weight of 0.27 (s.e. 0.06) (trial 2, year 1: fitting source of sire) and recommended selection following artificial rearing for improvement in lamb growth. As their co-heritability estimate was significantly higher than the estimate from this study, it may be useful to compare the details of the two trials (Table 5), (the 1st year of the second field trial of Owen *et al.* (1978) was used, as source of rams was confounded in the first field trial).

The different regression coefficients and accordingly different mean squares for ram family means from the two studies are unlikely to be attributable to management/environmental differences as the ram weights under artificial rearing and the progeny weights under natural rearing were similar in the two trials, as were the phenotypic variances for ram weight and for progeny weight. The Texel-Oxford and Suffolk crosses have similar growth rates over the period studied (Cameron and Drury, 1985) and the purebreeds have similar mature weights (93 and 91 kg respectively). Although the Texel-Oxford crosses were proportionately (0.02) heavier at 16 weeks than the Texel crosses, the difference did not approach statistical significance ( $P > 0.25$ ).

The magnitude of the selection differentials has no effect on the estimation of the regression coefficient, though it does affect the precision of the estimate. Despite the larger number of rams performance tested and rams selected in this trial, the precision of the estimates was no better than that found by Owen *et al.* (1978), due to the lower selection differential. The observed standard errors of the co-heritabilities for the two studies were as expected, using the formula of Hill (1970), given the selection differentials and number of rams performance tested and selected.

There seems no obvious explanation for the difference between the co-heritability

estimates for lamb weight from the two trials. Recent heritability estimates of weight for age with natural rearing have been low (e.g. 0.04 (s.e. 0.04) (Wolf *et al.*, 1981)) and the paternal half-sib heritability estimate from this trial was 0.09 (s.e. 0.06), adjusted to take account of the bias due to selection of the rams (Robertson, 1977). In retrospect, the estimate of Owen *et al.* (1978) seems rather high. However, it should be noted that the regression coefficients of progeny field performance on ram station performance from the 2 years of trial 2 of Owen *et al.* (1978) were 0.135 (s.e. 0.033) and 0.064 (no s.e.), when source of sire was fitted, even though 10 of the 20 rams used in the 1st year, were used in both years. If the genetic correlation for progeny field performance with ram station performance is significantly less than 1, then the co-heritability estimate may be lower than expected, due to the interaction between station and field performance. Such interactions have been common for growth rate in other species (e.g. Baker, Wickham and Morris (1982) in beef cattle and Standal (1984) in pigs).

For artificial rearing to be effective, the co-heritability ( $r_A h_1 h_2$ ) must be higher than the heritability for natural rearing ( $h_2^2$ ). For example, the co-heritability estimate of 0.27 from Owen *et al.* (1978; trial 2, fitting source of sire) could be achieved if there was no interaction ( $r_A = 1.0$ ), and would require  $h_1^2 = 0.73$  and  $0.36$  given  $h_2^2 = 0.10$  and  $0.20$ , respectively. These values would be multiplied by  $1/r_A^2$  for  $r_A < 1.0$ , giving extremely high values for  $h_1^2$  as  $r_A$  falls. Therefore, the results of this trial may be more realistic and consistent with other genetic parameter estimates for early lamb growth than those of Owen *et al.* (1978).

In the experiment, the co-heritability was similar to the heritability for natural rearing, which suggests that the advantage of reducing maternal effects on performance test is offset by the genetic correlation for natural and artificial rearing being markedly less than 1. Therefore, on the basis of this study, selection on ram 100-day weight with artificial rearing may not offer any advantage over natural rearing for improvement in lamb growth and carcass traits.

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# Design of multivariate selection experiments to estimate genetic parameters

N. D. Cameron and R. Thompson

AFRC Animal Breeding Research Organisation, West Mains Road, Edinburgh EH9 3JQ, Scotland

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**Summary.** The precision of estimates of genetic variances and covariances obtained from multivariate selection experiments of various designs are discussed. The efficiencies of experimental designs are compared using criteria based on a confidence region of the estimated genetic parameters, with estimation using both responses and selection differentials and offspring-parent regression. A good selection criterion is shown to be to select individuals as parents using an index of the sums of squares and crossproducts of the phenotypic measurements. Formulae are given for the optimum selection proportion when the relative numbers of individuals in the parent and progeny generations are fixed or variable. Although the optimum depends on "a priori" knowledge of the genetic parameters to be estimated, the designs are very robust to poor estimates. For bivariate uncorrelated data, the variance of the estimated genetic parameters can be reduced by approximately 0.4 relative to designs of a more conventional nature when half of the individuals are selected on one trait and half on the other trait. There are larger reductions in variances if the traits are correlated.

**Key words:** Experimental design – Genetic parameter estimation – Multiple traits – Selection – Canonical variates

## Introduction

Precise, unbiased estimates of genetic parameters, such as heritability and genetic correlations, are necessary to optimise breeding programs and to predict rates of change for various selection schemes. These parameters

can be estimated from the covariance among collateral relatives or from the regression of the progeny performance on that of their parents. Appropriate equations for the variances of these estimates obtained by such methods are well documented (e.g. Falconer 1981). Equations for calculating the variance of heritability estimates derived from single-trait selection experiments for various designs have been derived by Hill (1971).

One experimental design objective in single-trait selection experiments is to minimise the variance of the heritability estimate which is influenced by factors such as population size, selection intensity, family size, the genetic and phenotypic parameters and the number of generations of selection. Using prior information about the parameters of interest, efficient selection experiments can be designed to obtain precise, unbiased estimates of the parameters using the equations of Hill (1971).

When dealing with two or more traits, the genetic variances and covariances are parameters of interest and, as Thompson (1976) has noted, it is not obvious what the optimal design objective should be. Robertson (1959) and Tallis (1959) discussed the sampling variance of the genetic correlation coefficient and suggested that designs which are efficient for heritability estimation are also efficient for estimation of genetic correlations. For two traits, individuals in the parental generation could be split into two groups, selecting high and low within one group for trait  $X_1$  and selecting high and low within the other group for trait  $X_2$  (Reeve 1955) and studying either the regression of offspring traits on traits of the selected parents or the direct and correlated responses to selection. However, this may not be the most efficient design in an overall sense. Indices using both traits could be used as the selection criteria, rather than selecting directly on the traits measured. However, Gunsett et al. (1984) suggest a strong dependency of the design efficiency on the index weights used. We discuss these techniques for estimating genetic variances and covariances for two traits and compare the efficiencies of different selection designs.

We consider, in detail, two generation selection experiments when parental observations are only taken on one sex. A different experimental design to the classical high-low individual selection method is examined and it is shown to be more efficient and robust.

### Optimality criteria

Given a regression problem,  $Y = X\beta + e$ , where  $Y$  is a vector of the dependent variable,  $X$  is the design matrix for the independent variables and  $e$  is the vector of residuals with variance-covariance matrix  $V$ , then the confidence ellipsoid of the generalised least squares estimate  $\hat{\beta}$  of  $\beta$ ,  $\hat{\beta} = (X'V^{-1}X)^{-1}X'V^{-1}Y$ , with variance  $(X'V^{-1}X)^{-1}$ , has the form

$$[\beta: (\beta - \hat{\beta})' X' V^{-1} X (\beta - \hat{\beta}) < \text{constant}]$$

for any specified confidence coefficient. The content of the ellipsoid (e.g. volume in three dimensions) is proportional to  $|X'V^{-1}X|^{-1/2}$ . Therefore one design criterion is to minimise the content of the ellipsoid or to maximise  $|X'V^{-1}X|$ , the D-optimality criterion (Silvey 1980). The determinant of  $X'V^{-1}X$  will be denoted by  $\text{DET}(\beta)$ . The D-optimality criterion has the useful invariance property that if a design  $X$  maximises  $\text{DET}(\beta)$ , then the same design  $X$  also maximises  $\text{DET}(T^*\beta)$ , where  $T^*$  is a full rank transformation matrix. Therefore, a design that is optimal for estimation of  $\beta$  is also optimal for a linear transformation,  $T^*\beta$ , of  $\beta$ . There are other overall criteria; for example, to maximise the trace of  $X'V^{-1}X$  (the sum of the diagonal elements of the matrix) or to maximise the minimum eigenvalue of  $X'V^{-1}X$ , but these do not have this invariance property.

### Standardisation of traits

The genetic and phenotypic variance-covariance matrices for the traits will be denoted by  $G$  and  $P$ , respectively. We consider cases of standardised traits, with mean zero, when the diagonal elements of the  $P$  matrix are equal to one and assume that the traits are normally distributed. The methods and designs considered can be applied to multivariate data but are developed using bivariate data. The genetic variances and covariances of the standardised traits are then heritabilities ( $h_1^2$  and  $h_2^2$ ) and co-heritabilities ( $r_A h_1 h_2$  where  $r_A$  is the genetic correlation between the two traits). In the estimation of these parameters, it is convenient to work in terms of the vector  $\beta' = 0.5 [h_1^2 \ r_A h_1 h_2 \ h_2^2]$  rather than the  $(2 \times 2)$  symmetric matrix of genetic variances and covariances.

There is no loss of generality from standardising the traits, for if the diagonal elements of the  $P$  matrix are not equal to one, then the phenotypic variables can be standardised using a transformation,  $T^*$ , with the result that the genetic variance-covariance matrix of the transformed variables is  $T^* G T^{*'}$ . The invariance argument for D-optimality shows that a D-optimal design for the parameter  $\beta$  is also D-optimal for the parameters in  $T^* G T^{*'}$ .

Further, we assume that errors in the phenotypic matrix  $P$  can be neglected, either because there is adequate previous data or parental data on which to base estimation of  $P$ . The emphasis, within this paper, is on comparing estimation procedures and suggesting designs for genetic parameter estimation and so this assumption should have a negligible effect on the conclusions. Certainly, our formulation leads to known results on univariate heritability estimation.

### Estimation and design from response to divergent truncation selection

A common method of estimating genetic parameters for two traits, from divergent truncation selection experiments, is to have two selection groups using a different selection index in each group and measure the selection differentials and the correlated responses for the two traits on both selection indices (Falconer 1981). For each of the selection indices,  $I_m$  ( $m = 1, 2$ ), assume a total of  $M$  unrelated individuals are measured for both traits and a proportion  $p$  with the highest and  $p$  with the lowest index values are selected, such that  $pM = N$ . A total of  $RM$  progeny are reared and recorded and with equal family sizes there are  $n = R/2 p$  progeny per family. Let  $i$  and  $x$  be the expected selection differential and abscissa on the standardised normal curve corresponding to  $p$  and assume equal selection differentials in the two groups. Note that the upper and lower cases of the letter  $I$  denote different parameters, however this is standard notation (Falconer 1981).

Initially alternative estimation procedures and designs will be considered for fixed experimental resources. Later, optimisation of the selection proportion,  $p$ , family size,  $n$ , and the relative proportion of offspring generation measurements to parental generation measurements,  $R$ , will be discussed.

It is of interest to consider the possible combinations of selection weights for the two indices. If a selection index  $I_m = b_{1m} x_1 + b_{2m} x_2$ , then

$$\begin{aligned} I_m &\equiv (b_{1m}/\sqrt{b_{1m}^2 + b_{2m}^2}) x_1 + (b_{2m}/\sqrt{b_{1m}^2 + b_{2m}^2}) x_2 \\ &= x_1 \cos \theta_m + x_2 \sin \theta_m \end{aligned}$$

selects the same individuals, where  $x_j$  and  $b_{jm}$  are the standardised phenotypic values and index weights of the  $j^{\text{th}}$  trait for the  $m^{\text{th}}$  index respectively and  $\tan \theta_m = b_{2m}/b_{1m}$ . Each selection index is characterised by a single parameter  $\theta_m$ . By symmetry only the values of  $\theta_m$  in the range  $0^\circ$  to  $180^\circ$  need consideration. Graphically, the line  $x_1 \cos \theta_m + x_2 \sin \theta_m = 0$  makes an angle  $\theta_m$  with the  $x_1$  axis.

The expected genetic response,  $\Delta G_{jm}$ , in the progeny for trait  $j$  due to selection on index  $m$ , is given by the product of the regression of the additive genotype of the  $j^{\text{th}}$  trait on the phenotype of the  $m^{\text{th}}$  index and the selection differential ( $SD_m$ ) of the  $m^{\text{th}}$  index. Thus  $\Delta G_{jm} = 0.5 (b_{jm} \sigma_{jj} + b_{km} \sigma_{jk}) SD_m / \text{var}(I_m)$  where  $\sigma_{jj}$  and  $\sigma_{jk}$  are, respectively, the genetic variance for trait  $j$  and genetic covariance for traits  $j$  and  $k$  ( $j = 1, 2$ ;  $k = 3 - j$ ) and  $\text{var}(I_m)$  is the variance of the  $m^{\text{th}}$  index. The selection differential for the  $m^{\text{th}}$  index is calculated as the difference in mean index value between the high and low parental lines. The response in each trait can be estimated as the difference between the high and low progeny lines. The index weights  $b_{jm}$  are usually determined by biological arguments about the traits or the desired direction of the response (Eisen 1977). The responses of trait  $j$  in selection group  $m$  can be written in the form of a regression model, regressing responses in the two measured traits on selection differentials of the indices.

$$\begin{bmatrix} \Delta G_{1m} \\ \Delta G_{2m} \end{bmatrix} = \begin{bmatrix} b_{1m} SD_m / \text{var}(I_m) & b_{2m} SD_m / \text{var}(I_m) & 0 \\ 0 & b_{1m} SD_m / \text{var}(I_m) & b_{2m} SD_m / \text{var}(I_m) \end{bmatrix} \beta + [e]$$

or  $Y = X\beta + e$ . The model can also be defined in terms of selection differentials for each measured trait ( $SD_{jm}$ ),

$$\begin{bmatrix} \Delta G_{1m} \\ \Delta G_{2m} \end{bmatrix} = \frac{1}{(1 - r_p^2)} \begin{bmatrix} SD_{1m} - r_p SD_{2m} & -r_p SD_{1m} + SD_{2m} & 0 \\ SD_{1m} - r_p SD_{2m} & -r_p SD_{1m} + SD_{2m} \end{bmatrix} \beta + [e]$$

where  $r_p$  is the phenotypic correlation between the two traits. Alternatively, using the expected value of  $SD_m$ , the expected value of the design matrix  $X$  can be conveniently written using the angles  $\theta_m$ ,

$$\frac{2i}{\sigma_{I_m}} \begin{bmatrix} \cos \theta_m & \sin \theta_m & 0 \\ 0 & \cos \theta_m & \sin \theta_m \end{bmatrix} \quad (1)$$

for each index, where  $\sigma_{I_m}$  is the standard deviation of the  $m^{\text{th}}$  index.

The residuals within lines are correlated, due to the family structure of the design, but there is no correlation of residuals between lines. The  $4 \times 4$  variance-covariance matrix ( $V$ ) of the residuals is therefore symmetric and block diagonal

$$V = f \begin{bmatrix} F & 0 \\ 0 & F \end{bmatrix} \quad (2)$$

The matrix  $F$  represents the  $2 \times 2$  variance-covariance of a family mean after regressing on parental values and the factor  $f$  relates the variance of the mean genetic response for one index to the variance of a family mean. With response/selection differential estimation, there are  $N$  parents in each of the selected high and low lines, therefore  $f = 2/N$ .

The structure of  $F$  can be derived using the equations of Hill (1971) for the variance of residuals from single-trait selection. The variance for one progeny mean is

$$F = [(r_{oo} G - r_{op} G P^{-1} G r_{op}) + (P - r_{oo} G)/n] \quad (3)$$

where  $r_{oo}$  and  $r_{op}$  Wright's coefficients of relationship for progeny of the same parent and for progeny with parent respectively. Note that the first term in equation (3) is the variance of a family genotypic mean about the regression (drift variance) and the second term is the variance of measurement error in the family mean value. For example, in single-trait selection on parents of one sex with half-sib families

$$G = h^2, \quad P = 1.0, \quad r_{oo} = 0.25, \quad r_{op} = 0.5$$

and

$$F = [0.25 h^2 (1 - h^2) + (1 - 0.25 h^2)/n].$$

Gunsett et al. (1982, 1984) gave similar formulae for  $V$ , however their genetic drift term does not include any genetic relationship parameters ( $r_{oo}, r_{op}$ ) and their measurement error term does not have the divisor of the number of parents in each index.

Investigation of  $\text{DET}(\beta)$  and calculation of the inverse of  $V$  would be simpler if the matrix  $F$  was diagonal. As the matrix  $F$  is a function of the genetic and phenotypic variance-covariance matrices, transformation to independent traits would diagonalise  $F$ . Such a transformation exists and is often called a canonical transformation (Rao 1973). Let  $S^*$  be the transformation matrix from the original scale to the canonical scale, such that

$$\begin{bmatrix} C_1 \\ C_2 \end{bmatrix} = S^* \begin{bmatrix} x_1 \\ x_2 \end{bmatrix}$$



where  $C_1$  and  $C_2$  are the canonical traits which are phenotypically and genetically uncorrelated. Then  $S^*$  is such that  $S^*PS^*$  equals the identity matrix and  $S^*GS^* = G_C$  where  $G_C$  is the diagonal genetic variance-covariance matrix on the canonical scale. For half-sib family data, matrix  $F^{-1} = D$  becomes

$$D = \begin{bmatrix} d_1 & 0 \\ 0 & d_2 \end{bmatrix} \quad (4)$$

where  $d_j = (0.25 \lambda_j (1 - \lambda_j) + (1 - 0.25 \lambda_j)/n)^{-1}$  and  $\lambda_j$  denotes the canonical heritability of the  $j^{\text{th}}$  canonical trait.

If  $\beta_C$  is the vector of genetic parameters on the canonical scale, similar to  $\beta$ , and the indices on the canonical scale are  $I_1 = C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $I_2 = C_1 \cos \theta_{C2} + C_2 \sin \theta_{C2}$ , where  $\theta_{C1}$  and  $\theta_{C2}$  are the angles of the canonical selection indices, then  $\sigma_{Im} = 1$  and  $X'V^{-1}X_C$ , the value of  $X'V^{-1}X$  for canonical traits, is derived from equations 1 to 4

$$X'V^{-1}X_C = \begin{bmatrix} d_1 B_1 & d_1 B_3 & 0 \\ d_1 B_3 & d_1 B_2 + d_2 B_1 & d_2 B_3 \\ 0 & d_2 B_3 & d_2 B_2 \end{bmatrix}. \quad (5)$$

The expected value of  $\text{DET}(\beta_C)$  is

$$\text{DET}(\beta_C) = |X'V^{-1}X_C| \\ = d_1 d_2 (d_1 B_2 + d_2 B_1) (B_1 B_2 - B_3^2) \quad (6)$$

where

$$B_1 = 2N i^2 (\cos^2 \theta_{C1} + \cos^2 \theta_{C2}) \\ B_2 = 2N i^2 (\sin^2 \theta_{C1} + \sin^2 \theta_{C2}) = 2N i^2 (2 - B_1) \quad (7) \\ B_3 = N i^2 (\sin 2\theta_{C1} + \sin 2\theta_{C2}).$$

It can be shown that  $\text{DET}(\beta) = (1 - r_p^2)^{-3} \text{DET}(\beta_C)$  (see Appendix 1). In order to maximise  $\text{DET}(\beta_C)$ , it is differentiated with respect to  $B_2$  and  $B_3$ , and the maximum occurs when

$$\frac{B_2}{2N i^2} = \frac{-2(d_1 - 2d_2) \pm 2\sqrt{d_1^2 - d_1 d_2 + d_2^2}}{3(d_2 - d_1)} \quad (8)$$

and  $B_3 = \sin 2\theta_{C1} + \sin 2\theta_{C2} = 0$ , therefore  $\theta_{C2} = \theta_{C1} + 90^\circ$  or  $\theta_{C1} + \theta_{C2} = 180^\circ$ .

There are two cases to consider when maximising  $\text{DET}(\beta_C)$ . If the canonical heritabilities are equal,  $d_1$  equals  $d_2$ , then the maximum value of  $\text{DET}(\beta_C)$

occurs when  $B_2/2N i^2 = 1$  or  $\theta_{C2} = \theta_{C1} + 90^\circ$ . The indices on the canonical scale are  $I_1 = C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $I_2 = C_2 \cos \theta_{C1} - C_1 \sin \theta_{C1}$  and as this pair of axes are at right angles we call this an orthogonal design. The phenotypic covariance between the indices is zero. There are an infinite number of pairs of indices resulting in the maximum value of  $\text{DET}(\beta_C)$ .

If the canonical heritabilities are unequal, then  $\theta_{C1} + \theta_{C2} = 180^\circ$  and  $\theta_{C1}$  can be derived using equation (8) as  $B_2/2N i^2 = 2 \sin^2 \theta_{C1}$ . The indices on the canonical scale are  $I_1 = C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $I_2 = C_2 \sin \theta_{C1} - C_1 \cos \theta_{C1}$ . The lines  $I_1 = 0$  and  $I_2 = 0$  are symmetric about the  $C_1$  and  $C_2$  axes and we call this a symmetric design. Note that the angle between  $I_1$  and the  $C_1$  axis is equal to the angle between  $I_2$  and the  $C_1$  axis.

### Estimation and design from offspring-parent regression

The heritability of a trait can be estimated from the regression of progeny performance on parent performance, rather than using a summary of parental information and responses to selection. The design of experiments to estimate the heritability of a trait using offspring-parent regression have been discussed by Hill (1970) and Hill and Thompson (1977).

Offspring-parent regression techniques can be used to estimate genetic parameters of more than one trait simultaneously. The standardised observations on two traits for the  $j^{\text{th}}$  parent and the mean of its offspring are defined as  $x_{1j}$ ,  $x_{2j}$  and  $\bar{o}_{x1j}$ ,  $\bar{o}_{x2j}$ , respectively. Then

$$\begin{bmatrix} \bar{o}_{x1j} \\ \bar{o}_{x2j} \end{bmatrix} = 0.5 G P^{-1} \begin{bmatrix} x_{1j} \\ x_{2j} \end{bmatrix} + [e] \\ = 0.5 G \begin{bmatrix} s_{1j} \\ s_{2j} \end{bmatrix} + [e] \\ = \begin{bmatrix} s_{1j} & s_{2j} & 0 \\ 0 & s_{1j} & s_{2j} \end{bmatrix} \beta + [e]$$

where  $s_{1j}$  and  $s_{2j}$  are  $(x_{1j} - r_p x_{2j})/(1 - r_p^2)$  and  $(x_{2j} - r_p x_{1j})/(1 - r_p^2)$ , respectively.

Combining the information from all  $4N$  offspring-parents pairs,  $\beta$  can be estimated as before. The matrix  $V$  is now a  $8N \times 8N$  block diagonal matrix with the  $F$  matrix repeated  $4N$  times down the diagonal.

The contribution of each family to  $X'V^{-1}X$  can be expanded as

$$(X'V^{-1}X)_j = s_{1j}^2 \begin{bmatrix} D_{11} & D_{12} & 0 \\ D_{21} & D_{22} & 0 \\ 0 & 0 & 0 \end{bmatrix} + s_{1j} s_{2j} \begin{bmatrix} 0 & D_{11} & D_{12} \\ D_{11} & D_{12} + D_{21} & D_{22} \\ D_{21} & D_{22} & 0 \end{bmatrix} + s_{2j}^2 \begin{bmatrix} 0 & 0 & 0 \\ 0 & D_{11} & D_{12} \\ 0 & D_{21} & D_{22} \end{bmatrix} \quad (9)$$

where  $D_{jk}$  are the elements of  $F^{-1}$  (equation (3)). The sums of squares and crossproducts of the parental traits, after selection, are calculated using

$$\begin{aligned} & \text{cov}(x_1, x_2 \text{ selection on } I) \\ &= \text{cov}(x_1, x_2) - \frac{\text{cov}(x_1, I) \text{cov}(x_2, I)}{\text{var}(I)} \\ & \quad + \frac{\text{cov}(x_1, I) \text{var}(I^*) \text{cov}(x_2, I)}{\text{var}^2(I)} \\ &= \text{cov}(x_1, x_2) + \frac{i x \text{cov}(x_1, I) \text{cov}(x_2, I)}{\text{var}(I)} \end{aligned} \quad (10)$$

where  $\text{var}(I^*)$  is the variance of the index after selection. The sums of squares and crossproducts of  $s_{1j}$  and  $s_{2j}$ , after selection, can be determined from

$$\begin{bmatrix} \sum_{j=1}^{4N} s_{1j}^2 & \sum_{j=1}^{4N} s_{1j} s_{2j} \\ \sum_{j=1}^{4N} s_{1j} s_{2j} & \sum_{j=1}^{4N} s_{2j}^2 \end{bmatrix} = P^{-1} \begin{bmatrix} \sum_{j=1}^{4N} x_{1j}^2 & \sum_{j=1}^{4N} x_{1j} x_{2j} \\ \sum_{j=1}^{4N} x_{1j} x_{2j} & \sum_{j=1}^{4N} x_{2j}^2 \end{bmatrix} P^{-1} \quad (11)$$

As before, transformation on to the canonical scale results in the diagonalisation of the  $F$  matrix and  $X'V^{-1}X_C$  has the same structure as in equation (5), where now

$$B_1 = \sum_{j=1}^{4N} C_{1j}^2, \quad B_2 = \sum_{j=1}^{4N} C_{2j}^2 \quad \text{and} \quad B_3 = \sum_{j=1}^{4N} C_{1j} C_{2j} \quad (12)$$

with  $C_{1j}$  and  $C_{2j}$  being the observations on the canonical scale of the  $j^{\text{th}}$  selected parent and a total of  $4N$  selected individuals as before.  $\text{DET}(\beta_C)$  becomes

$$\text{DET}(\beta_C) = d_1 d_2 (d_1 B_2 + d_2 B_1) (B_1 B_2 - B_3^2)$$

which is of the same form as equation (6), with  $B_1$ ,  $B_2$  and  $B_3$  given by equation (12) rather than equation (7). The expected sums of squares and crossproducts of the observations can be rewritten as

$$B_1 = 2N [2 + i x (\cos^2 \theta_{C1} + \cos^2 \theta_{C2})]$$

$$B_2 = 2N [2 + i x (\sin^2 \theta_{C1} + \sin^2 \theta_{C2})]$$

$$B_3 = N i x [\sin 2\theta_{C1} + \sin 2\theta_{C2}].$$

Then

$$\text{DET}(\beta_C) = (2N)^3 d_1 d_2 [d_1 (2 + i x H) + d_2 (2 + i x (2 - H))] [2 + i x H] [2 + i x (2 - H)] \quad (13)$$

with  $H = \sin^2 \theta_{C1} + \sin^2 \theta_{C2}$ . In order to maximise  $\text{DET}(\beta_C)$ , it is differentiated with respect to  $B_2$  and  $B_3$ , and the maximum occurs when

and  $B_3 = \sin 2\theta_{C1} + \sin 2\theta_{C2} = 0$ , therefore  $\theta_{C2} = \theta_{C1} + 90^\circ$  or  $\theta_{C1} + \theta_{C2} = 180^\circ$ .

If the canonical heritabilities are equal,  $d_1$  equals  $d_2$ , then  $H$  equals one and  $\text{DET}(\beta_C)$  is maximised when  $\theta_{C2} = \theta_{C1} + 90^\circ$ . This corresponds to a ridge of points where  $\text{DET}(\beta_C)$  is of constant value (the previously mentioned orthogonal design). If the canonical heritabilities are not equal a symmetric design with  $2\sin^2 \theta_{C1} = H$ , found from equation (14), is again optimal.

The ratio of values of  $\text{DET}(\beta_C)$  from the orthogonal design using the offspring-parent regression and response/selection differential estimation is  $((2 + i x)/i^2)^3 > 1.0$ . For example, when  $p$  equals 0.10 and 0.20, the ratio equals  $(1.38)^3$  and  $(1.62)^3$ , respectively. The proportional gain in precision  $(2 + i x)$  from the offspring-parent regression designs comes from two sources. For example, if  $I_1 = C_1$  and  $I_2 = C_2$ , then  $(1 + i x)$  is proportional to the sums of squares for  $C_1$  from selection on  $I_1$  compared to  $i^2$  used in response/selection differential estimation. The remainder  $((2 + i x) - (1 + i x))$  is proportional to the sums of squares for  $C_1$  with selection on  $I_2$ , which is information not used in response/selection differential estimation.

Canonical traits have been used to simplify the development of the variance formulae and interpretation of the designs. When the experiment is being designed,  $G$  and hence the canonical transformation are not known precisely, therefore the specification of the optimal design is difficult. However, the class of orthogonal designs includes all pairs of indices that are phenotypically uncorrelated. On the standardised scale, an index  $I_2 = x_1 \cos \theta_{C2} + x_2 \sin \theta_{C2}$  can be found phenotypically uncorrelated to  $I_1 = x_1 \cos \theta_{C1} + x_2 \sin \theta_{C1}$ , if  $\tan \theta_{C2} = -(1 + r_p \tan \theta_{C1}) / (r_p + \tan \theta_{C1})$ . This gives some flexibility in the choice of designs. For example, the three pairs of indices  $I_1 = x_1$  and  $I_2 = x_2 - r_p x_1$ ,  $I_1 = x_2$  and  $I_2 = x_1 - r_p x_2$  and also  $I_1 = x_1 + x_2$  and  $I_2 = x_1 - x_2$  are members of the class of orthogonal designs. This choice of indices can be made without "a priori" knowledge of  $G$  and is optimal if the canonical heritabilities are equal.

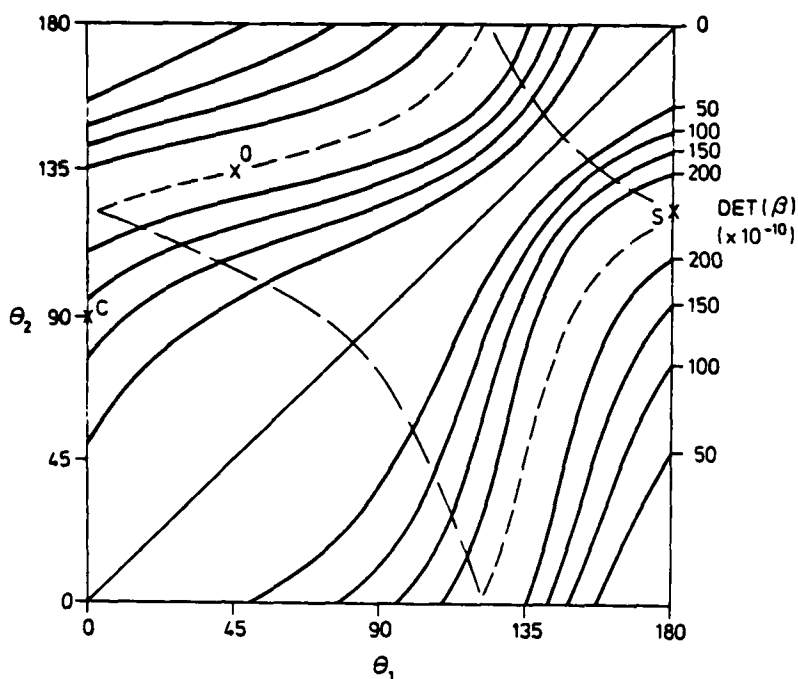
Manipulation of equations (13) and (14) shows that the ratio of  $\text{DET}(\beta_C)$  using the optimal symmetric design compared with using one pair from the above three indices is  $(1 + \eta \delta) / (1 - \eta^2)$  with

$$\eta = (-1 \pm \sqrt{1 + 3\delta^2}) / 3 = i x (H - 1) / (2 + i x)$$

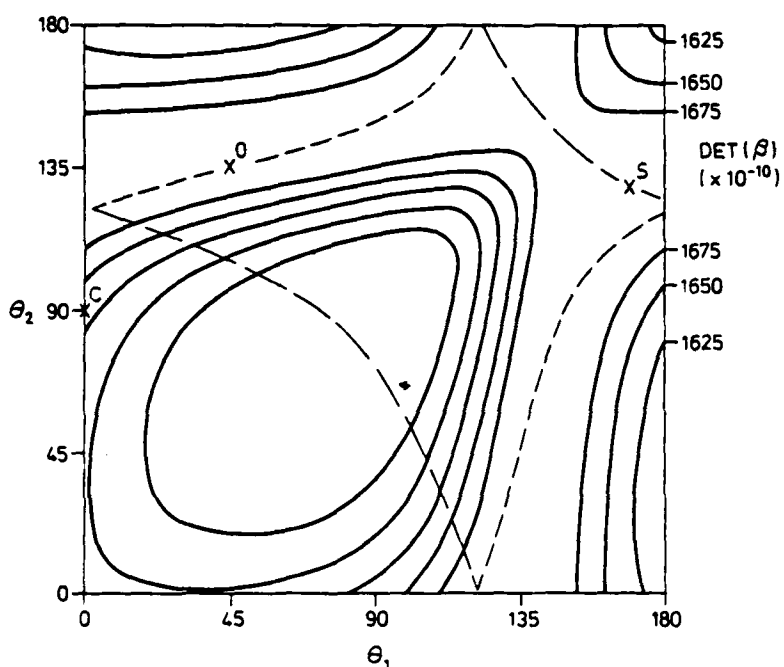
and  $\delta = (d_1 - d_2) / (d_1 + d_2)$ . For a range of canonical heritabilities, the ratio was generally less than 1.05.

$$H = \frac{-2[(d_1 - 2d_2) i x - (d_1 + d_2)] \pm 2(2 + i x) \sqrt{d_1^2 - d_1 d_2 + d_2^2}}{3 i x (d_2 - d_1)} \quad (14)$$





**Fig. 1.** Contours for  $\text{DET}(\beta)$  (divided by  $10^{10}$ ) for various linear indices of the traits defined by angles  $\theta_1$  and  $\theta_2$  with  $\beta$  estimated by response/selection differential. The classes of orthogonal designs (---), symmetric designs (—), the orthogonal design  $I_1 = x_1 + x_2$ ,  $I_2 = x_1 - x_2$  (O), the optimal symmetric design (S) and the classical design  $I_1 = x_1$ ,  $I_2 = x_2$  (C) are included



**Fig. 2.** Contours for  $\text{DET}(\beta)$  (divided by  $10^{10}$ ) for various linear indices of the traits defined by angles  $\theta_1$  and  $\theta_2$  with  $\beta$  estimated by offspring-parent regression. Classes of designs and individual designs are denoted as in Fig. 1

This suggests that the proportional increase in precision of a genetic variance or covariance estimate will be at most  $0.02 (= (1.05)^{1/3} - 1)$ , from using the symmetric design compared with using the orthogonal design. Therefore efficient selection indices can be constructed without estimates of the genetic parameters being available.

To illustrate these results, Figs. 1 and 2 show the contours for  $\text{DET}(\beta)$  estimated by response/selection differential (Fig. 1) and offspring-parent regression (Fig. 2). The heritabilities are 0.6 and 0.9 and the genetic and phenotypic correlations are 0.8 and 0.6, respectively, with 600 sires selected per index and a family size of 10 and selection proportion of 0.3, as used by Gunsett et al. (1984). Included are lines indicating the orthogonal designs with the same value of  $\text{DET}(\beta)$  (the orthogonal design  $I_1 = x_1 + x_2$ ,  $I_2 = x_1 - x_2$  is denoted by O) and the symmetric designs (the optimal symmetric design is denoted by S). The classical design  $I_1 = x_1$ ,  $I_2 = x_2$  is denoted by C ( $\theta_1 = 0^\circ$ ,  $\theta_2 = 90^\circ$ ). The contour for the orthogonal designs in Fig. 1 corresponds to the ridge noted by Gunsett et al. (1984). When  $\theta_1 = \theta_2$  in Fig. 1, then  $\text{DET}(\beta) = 0$  because only two parameters can be estimated. The orthogonal, symmetric and classical designs have values of  $\text{DET}(\beta)$  (divided by  $10^{10}$ ) of 233, 235 and 136 in Fig. 1 and 1,702, 1,719 and 1,635 in Fig. 2, respectively. The ratio  $1,702/233 = ((2 + ix)/i^2)^3 = 1.94^3$  shows the advantage of using offspring-parent regression with orthogonal designs.

When two linear indices are used to select parents, we have shown how to improve the precision of parameter estimates using offspring-parent regression. We have also shown how to choose the linear indices in an efficient way (viz. pairs of orthogonal indices on the canonical scale). We now consider an alternative selection criteria on which to select individuals.

### Elliptical selection experimental design

When using offspring-parent regression to estimate genetic parameters, the variance of the genetic parameters depends on the sum of squares of the observations on the parents. When only one trait is of interest, the sum of squares is maximised by selecting individuals with high and low values of the trait to be parents (i.e. selection of individuals with extreme values). By analogy, in the two dimensional case, this suggests selecting a proportion  $p_E$  (if the same experimental resources are used as in the divergent selection schemes, then  $p_E$  equals  $2p$ ) of the  $2M$  individuals measured which are as far from the origin as possible. Invariance arguments suggest using a quadratic index of the form  $(x_{1j} \ x_{2j})' P^{-1} (x_{1j} \ x_{2j})$  for the  $j^{\text{th}}$  individual. Geometrically, this can be thought of as selecting individuals outside an ellipse given by the formula  $(x_1 + x_2)^2/2(1 + r_p) + (x_1 - x_2)^2/2(1 - r_p) = w^2$ , where  $w$  is chosen such that a proportion  $p_E$  of the individuals are outside the ellipse and, because this depends on  $P$ , we call the ellipse a phenotypic selection ellipse.

Tallis (1963) considered this type of selection in a different context and showed that the proportion  $p_E$  and the variance-covariance matrix of the observations after elliptical selection,  $P^*$ , can be derived as  $p_E = F_2(w^2)$  and  $P^* = [F_4(w^2)/F_2(w^2)] P$  where  $F_k(w^2)$  is the probability that a  $\chi^2$  variable with  $k$  d.f. is greater than  $w^2$ . The recursive procedure of Hill and Pike (1966) gives the relationship between  $F_2(w^2)$  and  $F_4(w^2)$ , viz.  $F_4(w^2) = F_2(w^2) + (w^2/2) \exp(-w^2/2)$ , where  $F_2(w^2) = \exp(-w^2/2) = p_E$ . Therefore  $P^* = (1 - \log p_E) P$ .

As before, transformation onto the canonical scale results in the diagonalisation of the  $F$  matrix and  $\text{DET}(\beta_C)$  can be written as

$$\text{DET}(\beta_C) = (2M p_E)^3 d_1 d_2 (d_1 + d_2) (1 - \log p_E)^3. \quad (15)$$

The ratio of the determinants from elliptical selection and the orthogonal index design is  $(2(1 - \log p_E)/(2 + i x))^3 > 1.0$ . For example, when  $p_E$  equals 0.2 and 0.4, the ratio equals  $(1.23)^3$  and  $(1.21)^3$ , respectively, which shows the advantage of using the phenotypic selection ellipse rather than selecting on orthogonal canonical indices. Obviously, if no phenotypic selection is performed then  $p_E = 1.0$  and  $p = 0.5$  and the ratio of the two determinants is one.

The selection criteria  $(x_1 x_2)' P^{-1} (x_1 x_2) = w^2$  can be thought as  $(x_1 + x_2)^2/2(1 + r_p) + (x_1 - x_2)^2/2(1 - r_p) = w^2$  and  $x_1 + x_2$ ,  $x_1 - x_2$  are the axes of the ellipse. For canonical traits the selection ellipse reduces to a canonical circle which is generated by the orthogonal axes  $C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $C_2 \cos \theta_{C1} - C_1 \sin \theta_{C1}$ , for all values of  $\theta_{C1}$ . These axes are precisely those of the orthogonal indices suggested in the previous section. This naturally leads to the question if a canonical ellipse generated by the symmetric axes  $C_1 \cos \theta_{C1} + C_2 \sin \theta_{C1}$  and  $C_1 \sin \theta_{C1} - C_2 \cos \theta_{C1}$  can give a more efficient design. The calculation of the sums of squares and crossproducts for the parental values is more difficult and requires numerical integration (see Appendix 2 for calculation of  $\text{DET}(\beta_C)$ ). The maximum value of  $\text{DET}(\beta_C)$  occurred when the canonical ellipse was rotated by an angle  $\phi$  with values  $0^\circ$  and  $90^\circ$ , for  $0^\circ \leq \phi \leq 180^\circ$ . When  $\phi = 90^\circ$ , this corresponds to reparameterising  $C_1$  as  $C_2$  and vice versa. Therefore, the canonical ellipse generated by the symmetric axes gives the most efficient design.

Again there is the difficulty that these axes require estimates of  $G$  and we could not find an analytic formula for the optimal angle. The ratio of values of  $\text{DET}(\beta_C)$  from using the optimal symmetric and orthogonal axes depends on the proportion of individuals selected as parents. For combinations of canonical heritabilities in the range of 0.1 to 0.9 and a range of selection proportions ( $0.05 < p_E < 0.30$ ), the maximum value of the ratio was 1.01. The ratio decreased as the

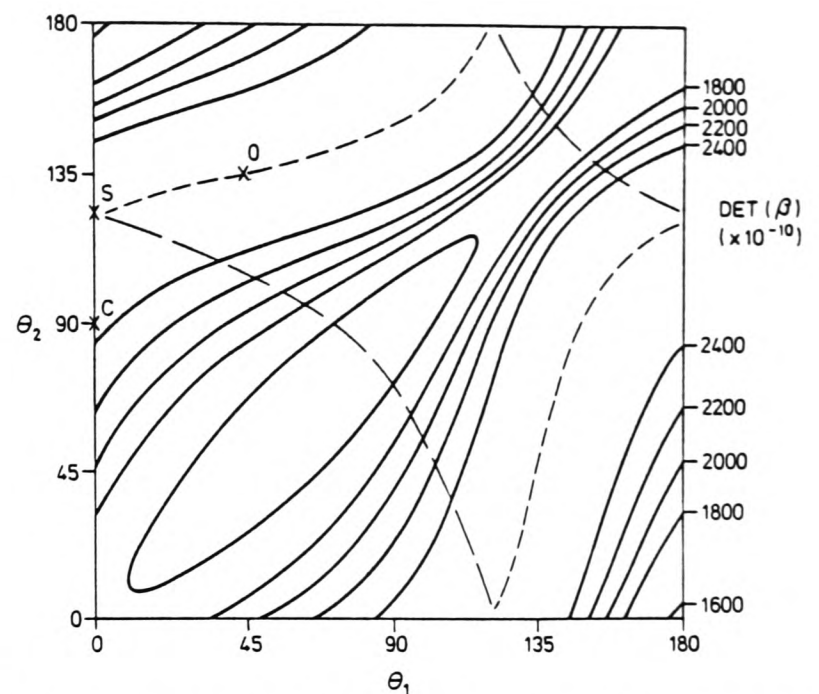


Fig. 3. Contours for  $\text{DET}(\beta)$  (divided by  $10^{10}$ ) for various quadratic indices of the traits defined by angles  $\theta_1$  and  $\theta_2$  with  $\beta$  estimated by offspring-parent regression. Classes of designs and individual designs are denoted as in Fig. 1

selection proportion increased and as the magnitude of the difference between  $\lambda_1(1 - \lambda_1)$  and  $\lambda_2(1 - \lambda_2)$  decreased. Therefore, there is a negligible loss of efficiency when using the phenotypic elliptical selection scheme compared with using the optimal elliptical scheme.

Figure 3 shows  $\text{DET}(\beta)$  using ellipses generated by axes  $I_1 = x_1 \cos \theta_1 + x_2 \sin \theta_1$  and  $I_2 = x_1 \cos \theta_2 + x_2 \sin \theta_2$  using the same  $G$  and  $P$  matrices and experimental facilities as in Figs. 1 and 2. The values (divided by  $10^{10}$ ) of  $\text{DET}(\beta)$  for the orthogonal (O), symmetric (S) and classical (C) axes are 2,650, 2,652 and 2,454, respectively, showing a marked increase over the corresponding values in Fig. 2, with

$$2,650/1,702 = (2(1 - \log p_E)/(2 + i x))^3 = (1.16)^3,$$

for the phenotypic selection ellipse.

#### Optimising the selection proportion, the family size and the ratio of individuals measured in the two generations

If the canonical heritabilities are equal, say to  $\lambda$ , the optimum proportion to select for maximising  $\text{DET}(\beta)$  with different estimation methods and selection designs can be found. For example, if  $\beta$  is estimated by response/selection differential the optimal  $p$  is found by differentiation of equation (6) with respect to  $p$ . The solution is given by

$$\frac{(1 - r_{oo} \lambda)}{R \lambda (r_{oo} - r_{op}^2 \lambda)} = \frac{2x - i}{4(i - x)p}$$

which suggests that  $p$  must be at least 0.27, that is when  $2x > i$ .

When estimating genetic parameters using offspring-parent regression, the optimal proportion  $p$  is obtained by differentiating equation 12 with respect to  $p$ , which satisfies

$$\frac{(1 - r_{oo}\lambda)}{R\lambda(r_{oo} - r_{op}^2\lambda)} = \frac{1 + x^2}{2p(1 + ix - x^2)} = W(2, p) \quad (16)$$

which is similar to that of Hill and Thompson (1977), derived in a univariate context,

$$\frac{(1 - r_{oo}\lambda)}{R\lambda(r_{oo} - r_{op}^2\lambda)} = \frac{x^2}{2p(1 + ix - x^2)} = W(1, p).$$

The minimum value of the right hand side of  $W(2, p)$  is one when  $p = 0.5$ , and all individuals are then used as parents. When using a phenotypic selection ellipse, differentiating equation (15) with respect to  $p_E$ , gives the result

$$\frac{(1 - r_{oo}\lambda)}{R\lambda(r_{oo} - r_{op}^2\lambda)} = \frac{-\log p_E}{p_E} = W(3, p_E). \quad (17)$$

These equations give an optimal design for fixed numbers of individuals in the parental,  $2M$ , and offspring,  $2MR$ , generations. If the balance of individuals in the two generations can be adjusted,  $R$ , then the optimal value of  $DET(\beta_C)/(2M(1+R))^3$ , a measure of the efficiency of the design on a per individual measured basis, can be determined. When divergent selection lines are used, the optimum value of  $p$  satisfies

$$\frac{(1 - r_{oo}\lambda)}{\lambda(r_{oo} - r_{op}^2\lambda)} = \left[ \frac{1 + x^2}{1 + ix - x^2} \right]^2 \frac{1}{2p} = W(4, p)$$

and  $R = (1 + x^2)/(1 + ix - x^2)$ . When the phenotypic selection ellipse is used, the optimum value of  $p_E$  satisfies

$$\frac{(1 - r_{oo}\lambda)}{\lambda(r_{oo} - r_{op}^2\lambda)} = (\log p_E)^2/p_E = W(5, p_E) \quad (18)$$

and  $R = -\log p_E$ . Figure 4 has been constructed to aid in the solution of the above equations, giving values of  $W(s, q)$  against the total proportion selected,  $p_T$ , where  $q = p_{T/2}$  for  $s = 1, 2$  and  $4$  and  $q = p_T$  for  $s = 3$  and  $5$ .

Since the genetic parameters are not known "a priori", designs should be robust to poor estimates of these parameters. The  $DET(\beta_C)$  values using elliptical selection were calculated for a range of equal canonical heritabilities, with fixed values of  $R$ , at fixed and optimum values of  $p_E$  and were then compared with  $DET(\beta_C)$  values when both the  $p_E$  and  $R$  are optimised (Fig. 5). The efficiency of designs when both  $p_E$  and  $R$  are optimised are shown as 100 and  $DET(\beta_C)$  values of other designs are shown relative to this base. Figure 5 indicates that for a wide range of canonical heritabili-

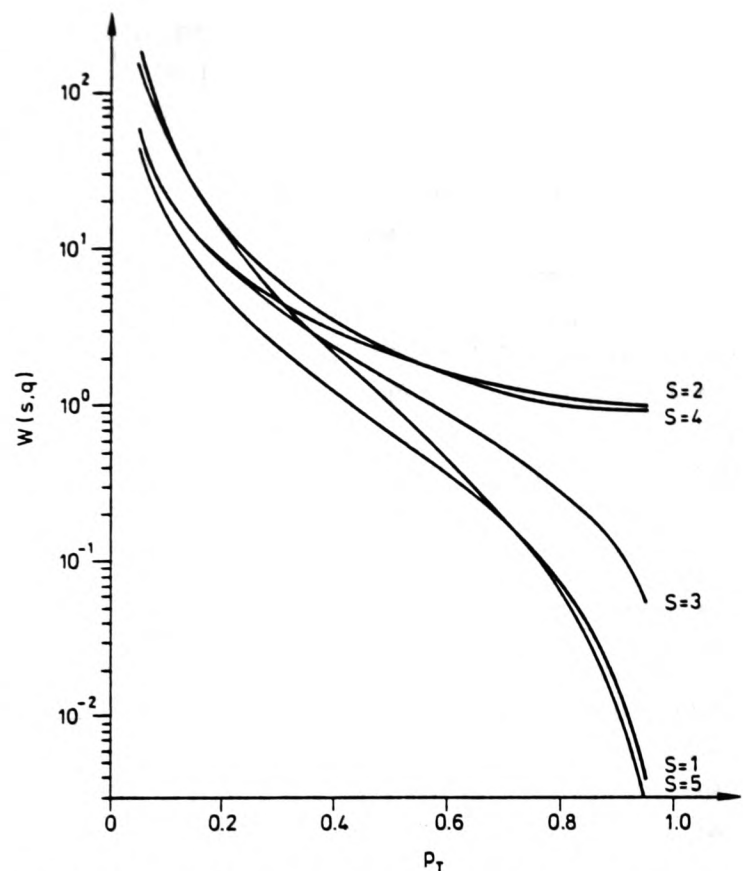


Fig. 4. Values of  $W(s, q)$  plotted against the total proportion selected,  $p_T$

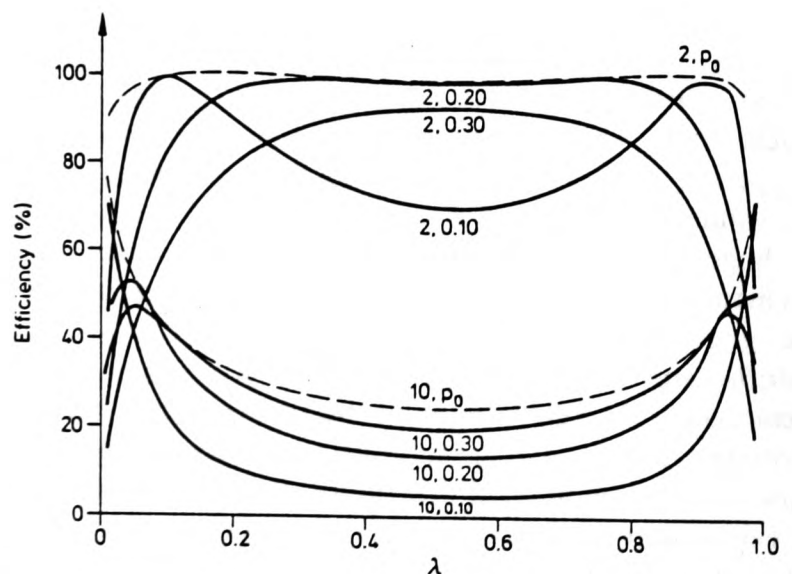


Fig. 5. Efficiency of alternative elliptical designs expressed as  $DET(\beta)$  for a fixed total number recorded relative to that when both  $p_E$  and  $R$  are optimised. Results are given for specified  $R$  and  $p_E$ , with  $p_E$  fixed or optimal ( $p_0$ )

ties, with  $R = 2$ ,  $p_E = 0.20$  is efficient. For example, with  $\lambda$  values in the ranges (0.18, 0.87) and (0.13, 0.90) designs using  $p_E = 0.20$  are at least 0.90 and 0.95 as efficient as the optimal design. When  $R = 10$ , designs are generally less than 0.40 as efficient as when  $R$  is optimised, although  $p_E = 0.30$  is close to the optimal value of  $p$ , for  $R = 10$ .

The optimum proportion of individuals to select as parents has been determined, but only when the

canonical heritabilities are equal. When the canonical heritabilities are unequal, one suggestion is to use a pooled value of  $\lambda$  in equations (16) to (18), with  $\lambda$  chosen such that the resulting  $d$  satisfies

$$2d^3 = d_1 d_2 (d_1 + d_2). \quad (19)$$

As there are two solutions to the quadratic equation for  $\lambda$ , we suggest using the  $\lambda$  value that lies between  $\lambda_1$  and  $\lambda_2$ . Due to some symmetry in the  $d$  value (i.e.  $\lambda(1-\lambda)$ ), the value of  $\lambda$  is less than 0.5 when  $\lambda_1 + \lambda_2 < 1$  and  $\lambda$  is greater than 0.5 otherwise. The value of  $\lambda$  satisfying equation (19) is essentially independent of the value of  $n$ , the number of progeny per parent, when  $n$  is moderate ( $> 15$ ). When no "a priori" estimates of the genetic parameters are available,  $n = 25$  seems a reasonable value to estimate  $\lambda$  with. The values of  $\text{DET}(\beta)$  calculated with the optimum  $p_E$  were regressed on the  $\text{DET}(\beta)$  values calculated using  $p_E$  derived from equation (17), for combinations of canonical heritabilities in the range 0.1 to 0.9 with various  $R$  and  $n$  values. If the methods of choosing  $p_E$  were identical, then the pooled regression coefficient and intercept are expected to have values 1.0 and 0.0 and the actual values were 0.980 and 0.003, respectively. Therefore, the use of equation (19) to generate a pooled  $\lambda$  value seems reasonable, for estimation of the optimum selection proportion,  $p_E$ .

### Extensions

The gains from using assortative mating when selection is practiced on both male and female parents in one dimensional problems have been demonstrated (Reeve 1955; Hill and Thompson 1977). The same results apply directly to multivariate designs with selection of mates being based on minimising the "phenotypic distance" between mates.

Selection over several generations can also be effective in increasing the precision. However, the distribution of the progeny measurements, the next parental generation, would not be normal which introduces further complications in the estimation of the variance of the parameters.

Estimation of genetic parameters with a selection ellipsoid is not just limited to two traits. For  $v (> 2)$  traits the phenotypic selection ellipsoid and transformation onto the canonical scale can be used as before. When the traits have equal canonical heritabilities, the determinant of the inverse of the variance-covariance matrix of the genetic parameter estimates, on the canonical scale, can be written as

$$\begin{aligned} \text{DET}(\beta_C) \\ = (v M p_E d [F_{v+2}(w^2)/F_v(w^2)])^{v(v+1)/2} 2^{v(v-1)/2}. \end{aligned}$$

The optimum proportion of individuals to select can be determined by differentiating  $v M p_E d F_{v+2}(w^2)/F_v(w^2) = v M p_E d K$  with respect to  $p_E$  in order to maximise the value of  $\text{DET}(\beta_C)$ , where  $K = F_{v+2}(w^2)/F_v(w^2)$ . However by defining the function  $W(p_E)$ , the optimal proportion is determined by solving

$$\frac{(1 - r_{oo}\lambda)}{R\lambda(r_{oo} - r_{op}^2\lambda)} = \frac{-1}{p_E} \left[ \frac{K}{p_E \partial K / \partial p_E} + 1 \right] = W(p_E)$$

where  $v M p_E$  is the total number of individuals selected for the ellipsoidal design. The mean parental sums of squares decreases as the number of traits increases and obviously as the proportion selected decreases. However marked gains for increasing the precision of estimates of genetic parameters can be made with at least 5 traits.

### An example

An example of a design using elliptical selection is taken from an ABRO sheep experiment to estimate genetic parameters for growth rate and carcass leanness in lambs slaughtered at fixed age. A total of 100 rams are measured and 750 progeny are expected, giving a  $R$  value of 7.5. The "a priori" estimates of the heritabilities are 0.20 and 0.40 and the genetic and phenotypic correlations are 0.25 and 0.15, respectively. The canonical traits are  $1.010 x_1 - 0.203 x_2$  and  $0.052 x_1 + 0.991 x_2$ , which are phenotypically uncorrelated and have phenotypic variance of 1.0. The canonical heritabilities are 0.192 (derived from  $1.010^2 h_1 + 2(1.010)(-0.203) r_A h_1 h_2 + (-0.203)^2 h_2^2$ ) and 0.401, and using  $n = 25$  to estimate  $\lambda$ , the value of 0.262 is derived from equation (19). Given the  $R$  value of 7.5, the optimum proportion of rams to select,  $p_E$ , is 0.378 from solving  $W(3, p_E) = (-\log p_E)/p_E = 2.57$  (equation (17)) or using Fig. 4, and so each selected ram has an expected 20 progeny. Therefore 38 rams are selected such that  $x_1^2 + 2(-0.15)x_1 x_2 + x_2^2 > 1.94(1 - 0.15^2)$  where  $x_i$  are the standardised measurements of growth rate and carcass leanness. The value of  $w^2 = 1.94$  is derived from  $p_E = \exp(-w^2/2)$ .

The matrix  $X'V^{-1}X_C$  on the canonical scale can be derived using equations (5) and (12) and is diagonal with elements 866, 1,578 and 712 using  $d_1 = 11.58$  and  $d_2 = 9.52$  with  $B_1 = B_2 = 38(1 - \log 0.38)$  and  $B_3 = 0$ . Appendix 1 derives the matrix  $R^*$  such  $R^* \beta = \beta_C$ , and in this case

$$R^* = \begin{bmatrix} 0.102 & -0.411 & 0.041 \\ 0.053 & 0.990 & -0.202 \\ -0.003 & 0.104 & 0.982 \end{bmatrix}.$$

The variance-covariance matrix of the genetic parameter estimates is then

$$4(R^*)^{-1}(X'V^{-1}X_C)^{-1}((R^*)^{-1})' = 4 \text{var}(\beta)$$

$$= \begin{bmatrix} 46.4 & 7.8 & 1.3 \\ 7.8 & 26.0 & 8.7 \\ 1.3 & 8.7 & 56.0 \end{bmatrix} \times 10^{-4}.$$

The expected standard errors for the heritabilities of 0.20 and 0.40 are 0.068 and 0.075, respectively and for the genetic covariance of 0.064 the standard error is 0.051.

If the rams were split into two groups and selected high and low in each group, using an orthogonal design, then the



variances of the genetic parameter estimates are proportionately increased by 1.21 (derived from  $2(1 - \log p_E)/(2 + i x)$ ) compared to using elliptical selection. If only information on the parental selection traits is used, then the proportional increase is larger, 1.75 from  $2(1 - \log p_E)/(1 + i x)$ .

If the classical design is used to estimate the genetic parameters, then the matrix  $X'V^{-1}X$ , determined from equations (9) and (10), equals

$$\begin{bmatrix} 743 & -187 & 11 \\ -187 & 1.381 & -175 \\ 11 & -175 & 616 \end{bmatrix}$$

using  $D_{11} = 11.85$ ,  $D_{22} = 9.83$  and  $D_{12} = D_{21} = -1.88$  with

$$\sum_{j=1}^{38} x_{1j}^2 = \sum_{j=1}^{38} x_{2j}^2 = 19(1 + i x) + 19(1 + i x (0.15)^2) = 62.36$$

and

$$\sum_{j=1}^{38} x_{1j} x_{2j} = 12.84.$$

Then

$$\sum_{j=1}^{38} s_{1j}^2 = \sum_{j=1}^{38} s_{2j}^2 = 62.7 \quad \text{and} \quad \sum_{j=1}^{38} s_{1j} s_{2j} = -5.83$$

from equation (11). The variance-covariance matrix of the genetic parameters is then  $4 \text{ var}(\beta)$ , as before, and equals

$$\begin{bmatrix} 55.8 & 7.7 & 1.2 \\ 7.7 & 31.1 & 8.7 \\ 1.2 & 8.7 & 67.4 \end{bmatrix} \times 10^{-4}.$$

Therefore, the proportional increase in the variance of the genetic parameter estimates using the classical design compared to the elliptical design is 1.22.

Note that the matrix of weights on the original scale contributing to the selection indices (B) can be determined from the matrix of weights on the canonical scale ( $ANG_C$ ). If selection is on the orthogonal canonical indices  $I_1 = C_1 + C_2$  and  $I_2 = C_1 - C_2$ , such that  $\theta_{C1} = 45^\circ$  and  $\theta_{C2} = 135^\circ$ , then

$$ANG_C = \begin{bmatrix} \cos \theta_{C1} & \sin \theta_{C1} \\ \cos \theta_{C2} & \sin \theta_{C2} \end{bmatrix} = \begin{bmatrix} 0.707 & 0.707 \\ -0.707 & 0.707 \end{bmatrix}$$

and

$$B = ANG_C S^* = \begin{bmatrix} 0.751 & 0.557 \\ -0.677 & 0.844 \end{bmatrix}$$

Equivalent indices are

$$\begin{bmatrix} \cos \theta_1 & \sin \theta_1 \\ \cos \theta_2 & \sin \theta_2 \end{bmatrix} = \begin{bmatrix} 0.803 & 0.596 \\ -0.626 & 0.780 \end{bmatrix}$$

and the angles of the indices on the original scale are  $36.6^\circ$  and  $128.8^\circ$ .

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**Appendix 1**

The value of  $DET(\beta)$  can be determined from  $DET(\beta_C)$ . Since  $G_C = S^* G S^{*'}$ , then

$$\beta_C = 0.5 \begin{bmatrix} G_{C11} \\ G_{C12} \\ G_{C22} \end{bmatrix} = \begin{bmatrix} S_{11}^{*2} & 2S_{11}^* S_{12}^* & S_{12}^{*2} \\ S_{11}^* S_{21}^* & S_{11}^* S_{22}^* + S_{21}^* S_{12}^* & S_{12}^* S_{22}^* \\ S_{21}^{*2} & 2S_{21}^* S_{22}^* & S_{22}^{*2} \end{bmatrix}.$$

Let the above  $3 \times 3$  matrix be denoted  $R^*$ , then

$$\beta_C = R^* \beta \quad \text{and} \quad \beta = (R^*)^{-1} \beta_C$$

$$\text{var}(\beta) = (R^*)^{-1} \text{var}(\beta_C) ((R^*)^{-1})'$$

$$\text{var}(\beta)^{-1} = R^* \text{var}(\beta_C)^{-1} R^{*'}$$

$$|X'V^{-1}X| = |R^*|^2 |X'V^{-1}X|_C.$$

As  $S^* P S^{*'} = I$ , then  $|S^*|^{-2} = |P| = (1 - r_p^2)$ . The determinant of  $R^*$  can be shown to equal  $|S^*|^3$ , therefore

$$DET(\beta) = (1 - r_p^2)^{-3} DET(\beta_C).$$

**Appendix 2**

In this appendix the calculation of  $p_E$  and the mean sums of squares and crossproducts after elliptical truncation selection is illustrated. The selection ellipse based on symmetric axes is  $C_1 \cos \theta + C_2 \sin \theta$  and  $C_1 \cos \theta - C_2 \sin \theta$  is  $a^2 C_1^2 + b^2 C_2^2 = w^2$ , where  $C_1, C_2$  are the canonical variates and  $a^2 = 2 \cos^2 \theta$ ,  $b^2 = 2 \sin^2 \theta$ . Given the proportion to be selected,  $p_E$ , the

"size" of the ellipse,  $w$ , satisfies

$$p_E = 1 - \frac{4}{\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} \exp(-C_1^2/2) \int_0^{C_2(C_1)} \frac{1}{\sqrt{2\pi}} \exp(-C_2^2/2) dC_2 dC_1$$

where  $C_2(C_1) = \sqrt{(w^2 - a^2 C_1^2)/b^2}$ . Likewise the mean sum of squares and crossproducts of the canonical variates after elliptical selection are given by  $SS_1(\theta)$ ,  $SS_2(\theta)$  and  $CP(\theta)$

$$p_E SS_1(\theta_1) = 4 \left[ \frac{1}{\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} C_1^2 \exp(-C_1^2/2) \int_{C_2(C_1)}^{\infty} \frac{1}{\sqrt{2\pi}} \exp(-C_2^2/2) dC_2 dC_1 + \frac{1}{\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} C_1^2 \exp(-C_1^2/2) 0.5 dC_1 \right]$$

with  $SS_2(\theta_1) = SS_1(90^\circ - \theta_1)$  and by symmetry  $CP(\theta) = 0$ . By integrating by parts,

$$p_E SS_1(\theta_1) = 4 \left[ \frac{1}{2} \int_0^{\sqrt{aw^2}} C_1^2 \exp(-C_1^2/2) p_2 dC_1 + xz + p_1 \right] \quad (A1)$$

where

$$p_1 = \frac{1}{2\sqrt{2\pi}} \int_0^{\sqrt{aw^2}} \exp(-C_1^2/2) dC_1 \quad \text{and}$$

$$p_2 = \frac{1}{\sqrt{2\pi}} \int_{C_2(C_1)}^{\infty} \exp(-C_2^2/2) dC_2$$

and  $z$  is the height of the ordinate at truncation point  $x$ . If the indices of the selection ellipse are defined by angles  $\theta_{C_1}$  and  $\theta_{C_2}$ , the ellipse can be written as:

$$w^2 = (C_1 \cos \theta_{C_1} + C_2 \sin \theta_{C_1})^2 + (C_1 \cos \theta_{C_2} + C_2 \sin \theta_{C_2})^2$$

or

$$w^2 = 2u^2 \cos^2((\theta_{C_1} - \theta_{C_2})/2) + 2v^2 \sin^2((\theta_{C_1} - \theta_{C_2})/2)$$

where

$$u = C_1 \cos((\theta_{C_1} + \theta_{C_2})/2) + C_2 \sin((\theta_{C_1} + \theta_{C_2})/2)$$

$$v = C_1 \cos((\theta_{C_1} + \theta_{C_2} + 180^\circ)/2) + C_2 \sin((\theta_{C_1} + \theta_{C_2} + 180^\circ)/2)$$

which is the equation of an ellipse on a scale with orthogonal axes  $u$  and  $v$ . The sums of squares of  $u$  and  $v$  ( $SS_u$  and  $SS_v$ ) can therefore be calculated using equation (A1). By transforming back to the canonical scale, the mean sums of squares and crossproducts of the canonical variates are

$$SS_1 = SS_u \cos^2((\theta_{C_1} + \theta_{C_2})/2) + SS_v \sin^2((\theta_{C_1} + \theta_{C_2})/2)$$

$$SS_2 = SS_u \sin^2((\theta_{C_1} + \theta_{C_2})/2) + SS_v \cos^2((\theta_{C_1} + \theta_{C_2})/2)$$

$$CP = (SS_u - SS_v) (\sin(\theta_{C_1} + \theta_{C_2}))/2.$$