THE ESTIMATION OF RESPONSES TO SELECTION IN HILL SHEEP

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DECLARATION

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

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. ABSTRACT

A selection experiment with Scottish Blackface sheep was started by the Animal Breeding Research Organisation in 1956. Three lines, of approximate annual size of 270 ewes and 10 rams, were maintained until 1974, in which selection was at random or for high and low values of an index of cannon bone length at 8 weeks of age adjusted for body weight at the same age. An unselected base flock (1954-55) and the randomly selected line were used to estimate base population parameters while the selected lines were used to estimate realised responses to selection in both selected and correlated traits. The aims of the study were to compare predicted and realised responses to selection and to estimate genetic parameters of lifetime productivity in Scottish Blackface sheep.

Predicted responses were based on estimates of heritabilities and genetic correlations largely from paternal half-sib analyses of variance. Realised responses to selection were estimated from the regression of response on selection differential. The expected variance-covariance matrix of observed responses was included in generalised least-squares estimates of these regressions.

The realised heritability of the index under selection, estimated from the divergence of selected lines, was 0.52±0.02. After allowing for the expected reduction in heritability arising from linkage disequilibrium, this was almost exactly equal to the base population estimate of 0.56±0.04. The responses in the component traits of the index were also very close to those expected from base population parameters.

Selection for increased cannon bone length, adjusted for body weight, resulted in (i) increased body weights at all ages between birth and maturity, (ii) increased reproduction rate, principally from increased litter size but also from small responses in ewe fertility and lamb survival and (iii) decreased survival of adult ewes. The realised genetic correlations were relatively small (up to 0.3) but mostly significantly different from zero, whereas base population genetic correlation estimates were very imprecise. The realised responses in reproduction rate were accounted for by the response in body weight.

The genetic analysis of lifetime economic traits indicated the scope that exists for improving Scottish Blackface Sheep. Expected responses from some alternative selection strategies were derived and the implications discussed. The most important conclusions were: (i) the importance of maternal environment on performance arising from both the behaviour and management of the ewes, (ii) carry-over effects between ages, (iii) lower than expected genetic correlations between body weight at different ages, and (iv) the high genetic correlation between litter size and mature body size.

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CHAPTER 1

INTRODUCTION

Selection experiments have been used extensively in laboratory species for many traits so that the consequences of selection may be directly observed. Such consequences include the rate and duration of response to selection, genetic associations with other traits and long-term changes in genetic variance from both a decline due to fixation of favourable alleles and an increase from new mutations. Among farm animals, and sheep in particular, the use of selection experiments is necessarily more limited because such experiments are costly in terms of animals required and very long-term due to the slow turnover of generations. Thus, predictions of likely rates of response in traits of interest in sheep are usually based on parameter estimates from unselected flocks. These predictions are strictly applicable to one cycle of selection only but, with a number of implicit assumptions, the predictions are usually extended to a number of generations. Where they have been established, selection lines in sheep represent an opportunity for directly observing selection responses and testing some of the assumptions upon which the predictions of response are based.

This thesis is concerned with both the prediction and estimation of responses to selection in Scottish Blackface sheep. Information was available on unselected and selected lines of animals within a large selection experiment conducted by the Animal Breeding Research Organisation, Edinburgh over a twenty year period. Initially, selection experiments in sheep will be reviewed with respect to design, analysis and interpretation. The added complexity of overlapping generations in sheep will be particularly highlighted. The experimental part of the thesis is in four separate chapters:-

*prediction of likely rates of response from base population parameters. The various genetic and environmental components of phenotypic variance in the characters of interest will be established.

*realised responses to selection in the selected trait will be estimated and compared with prediction.

*estimation of base population parameters for the components of lifetime productivity including measures of body weight growth throughout life, survival, reproduction rate and wool production. These parameters are required to aid interpretation of realised correlated responses to selection. Additionally, however, these analyses will provide the basis for establishing breeding plans for the improvement of economically important traits in Scottish Blackface sheep.

*estimation of predicted and realised correlated responses to selection in the components of lifetime productivity.

CHAPTER 2

SELECTION EXPERIMENTS IN SHEEP: A REVIEW OF DESIGN, ANALYSIS AND RESULTS

INTRODUCTION

Selection experiments have been used extensively in the study of quantitative genetics of sheep populations. Their first reported use was just prior to 1950, at a time when such experiments were not very widespread even among laboratory animals. At about this time several sets of experiments were initiated in Australia, New Zealand and the United Kingdom. Since then, a number of other experiments have commenced although they have generally not been of the same scale as the original experiments, with the exception of a series of large selection lines started in New Zealand about 1970. The experiments reported in the literature had diverse aims but were principally concerned with quantification of rates of direct response to selection over time and estimation of correlated changes.

An appropriate theoretical basis for the design and analysis of selection experiments is of much more recent origin. Early discussion of the subject largely ignored the fact that a selection line is sampled from a population of possible selection lines so that there is, at least, a hypothetical variance between lines selected for the same objective. To ignore such between-line variance will increase the 'apparent' precision of realised responses to selection observed in a single selection line. This led Hill (1980) to conclude that "whilst selection experiment can give a lot of useful information, a naive design and analysis gives the impression that the experiment conveys more information that it actually contains".

In the light of past experience, then, how useful have sheep selection experiments been and what difficulties have they exposed? In this review we are less interested in critically reviewing past interpretation or studying practical relevance, but more in highlighting some issues that have arisen which may be of importance to the future design and analysis of such experiments. Firstly, the principles of design and analysis of selection experiments with particular reference to sheep populations will be briefly reviewed. Secondly, the scope and features of many selection experiments in sheep will be described and the implications of some results will be discussed.

AIMS OF EXPERIMENTS

Selection experiments can have a variety of aims and Hill (1980) has listed some aims for short- and long-term experiments. The selection criterion can be a single trait, either based on a single measurement or on information from more than one source (for example, information from relatives), or multiple traits combined together in some form of index. The term 'index' is used in its widest sense of some method of combining information and is not meant to imply the formal use of a selection index as distinct from other methods, such as independent culling levels on two or more traits. The index itself may be thought of as an individual trait under some conditions. In that case the experiment would be best described as a single trait line in which direct responses in the index and correlated responses between other traits (including the index components) and the index would be observed.

The objectives of most sheep selection experiments can be grouped into the following categories. Of course, these objectives are not all mutually exclusive and several experiments commenced with one specific aim and, with time, have been used to provide information in several other areas.

(i) Experimental check on theoretical predictions of genetic progress in both the selected and correlated traits. Theoretical predictions were usually made from base population heritabilities and genetic correlations, estimated by analyses of parents and offspring and/or collateral relatives. Commonly single trait selection lines have been established in which it was planned to measure direct response to selection and correlated responses in traits of economic importance. For example, Turner (1977) listed numerous single character selection lines in Merino sheep that were established in Australia by CSIRO at Cunnamulla and the New South Wales Department of Agriculture at Trangie in about 1950. These experiments were all designed to give information on experimental responses to selection in economically important traits in Merino sheep, principally concerned with wool production and its component traits. Purser (1967) described single character selection lines in British hill sheep involving selection on body conformation, fleece medullation and birth coat that were designed principally to produce experimental comparisons of observed and predicted responses to selection. In addition, some multi-trait selection lines have been established for this objective. Turner and Jackson (1978) reported the results of two large flocks selected principally for fleece weight with restrictions on genetic progress in several other traits. Similarly, Ercanbrack, Price and Terrill (1968) selected on an index aimed at improving the aggregate genotype for overall economic merit.

(ii) Direct selection on a trait to test whether the trait exhibits genetic variance, and then to estimate realised heritability from the experiment. The only difference between this aim and the previous one is that there is no predicted rate of response since the heritability of the trait is unknown. The classical example in sheep of such an experiment was the selection lines established in the New Zealand Romney at Ruakura in 1948 to select for high and low incidence of twinning. The flocks and some responses to selection were described by Clarke (1972). Similar selection lines were established in the Australian Merino by CSIRO in 1954 (Turner 1978).

(iii) Estimation of genetic covariances between the trait under selection and other potentially correlated traits. Again, this only differs from the first objective in that we have no prior prediction of the genetic covariance to be estimated. There are two principal areas in which this type of design is becoming increasingly used:

* <u>indirect selection</u>. For selection objectives such as reproduction rate or disease resistance, prediction of genetic merit from phenotype is often difficult. This has provided the incentive to find indirect characters, more easily measurable, that may increase expected responses to selection. Two approaches have been adopted. Firstly, selection has been based on an indirect physiological trait and correlated response in the character of interest measured. For example, Land, Carr and Lee (1980) selected

for testis size in males and estimated the correlated response in female reproduction rate, while Piper and Bindon (unpublished) have selected for ovulation rate and measured correlated response in litter size. Secondly, selection can be used to develop divergent lines in the trait of interest and, subsequently, the correlated responses in various indirect physiological traits may be estimated. For example, McGuirk _et al_ (1978) reported the commencement of an experiment to create divergent lines for susceptibility to fleece rot in Merino sheep as a means of finding potentially useful indirect criteria of selection. Similarly, Land _et al_ (1982) suggested the establishment of lines of sheep selected for the major reproductive components to assist the search for indirect selection criteria.

*_physiological understanding_. The selection experiments of Wiener (1982) for plasma copper levels and Piper (unpublished, CSIRO Division of Animal Production Research Report 1982) for resistance to helminth infection were both designed with a view to understanding physiological mechanisms. Similarly, McGuirk (1980) reviewed the physiological and biochemical responses observed from comparisons of divergent selected lines for fleece weight in Merino sheep.

(iv) Comparison of rates of response in alternative breeding programmes. Dalton and Baker (1980) briefly described an integrated set of selection lines established in New Zealand across breeds and locations in the early 1970's. The lines include selection for single traits and index selection for combinations of traits. The marginal response in overall economic merit arising from including a trait into an index is one of the questions being posed by this experiment.

(v) Study of genotype x environment interaction. Lines selected for the same trait in two different locations have been reported by Osman and Bradford (1965) for weight at weaning, Bradford (1972) for litter size and Turner (1977) for fleece weight. Measurement of responses in each environment will give estimates of heritability appropriate to that environment and responses of each line measured in both environments can give estimates of the realised genetic correlation. A less precise test of genotype x environment interactions can be obtained from a comparison of divergent lines selected in a single environment but tested in different environments. Hamilton and Langlands (1969) have reported such an experiment with lines selected for and against fleece weight.

(vi) Tests of linearity of direct and correlated responses. Predictions of responses to selection are based on assumed linearity of response in either direction of selection. Where divergent selection lines with a control have been established, the design implies that this assumption of linearity of response will be tested. The large scale single-trait lines listed under objective (i) were almost all divergent selection lines for each trait with a randomly selected control and so provide some test of linearity of response.

DESIGN OF EXPERIMENTS

Despite the multiplicity of specific aims, all selection experiments are concerned with the measurement of a selection response and an estimate of the precision of this response. We require the estimate of response to be unbiassed by environmental trends or fluctuations. There are a number of alternative methods available to estimate genetic trend and these vary in cost and precision. A detailed discussion of several of these methods has been produced by Hill (1972c).

(i) Control population. Maintenance of a randomly selected control line is designed to give a continuous measure of the environmental mean for all measured characters from which genetic responses, both direct and correlated, can be assessed. A secondary purpose of control lines has been to estimate genetic variances for correlated traits from information on related individuals. A major disadvantage of a control line is that it requires large resources, although in many sheep experiments a single control line has been used for more than one selection line.

(ii) 'Occasional' control. The development of technology for freezing embryos will open the way for generating a control population when it is required rather than continually maintaining a line. The obvious advantage of such an 'occasional' line is to reduce the resources required to maintain the control. In addition, the effective population size of the line, and therefore genetic drift and inbreeding, may be more easily minimised in this situation. While responses to selection would only be measured at intervals with such a control, this will have little effect on the precision of the estimate since it will be shown that annual (or continuous) measures of response become increasingly correlated with each other and so provide less and less independent information. Such a control will require specialised facilities for collection and storage of embryos but it is conceivable that such costs could be less than the cost of maintaining a continuous control line.

(iii) Divergent selection. A pair of lines selected for high and low values of a trait is usually a more efficient design for a selection experiment than a selected line and a control. Contemporaneous comparison of the lines gives an estimate of genetic divergence that is unbiased by environment fluctuations and, with the same total resources, is twice that of the deviation of a selected line from a control. The disadvantages of divergent selection lines are that symmetry of response in the two directions is assumed and that the downward selection line may be of no practical significance.

(iv) Repeat matings. Contemporary comparisons of the progeny of old and young sires can give a measure of response to selection. Mann, Ponzoni and Polkinghorne (1980) reported an experiment where overlapping sires were used to estimate responses, and they discuss the method. Unless the sires are markedly different in age, the expected differences in their progeny due to selection response are very small and imprecisely measured. However, increasing the age to which old sires are kept also reduces the total response to selection. Further, any selection amongst young sires can seriously bias the estimate of genetic trend.

(v) Mixed model methods. Henderson (1973 et seq) has developed analytical methods for separating genetic and environmental trends within a selected population using the genetic relationships between animals within that population. Blair and Pollak (1984) have used such an approach in the analysis of a selection experiment for fleece weight. Since this is more appropriately a method of analysis it will be discussed later.

The precision of estimated response to selection is a function of the design of the experiment. Hill (1980) has extensively reviewed appropriate features for the design of selection experiments. The important elements of design are discussed in terms of their expected effect on the variances of selection responses. In particular, the precision of estimated parameters from a selection experiment is determined by effective population size, duration of experiment, selection intensity and expected genetic variance of the trait (or genetic covariance between two traits). The expected variance of response at each generation is derived from the variance due to genetic drift and the measurement error variance. Drift variance arises principally from the genetic sampling of individuals from one generation to become the parents of the next generation and so accumulates across generations. Measurement error variance is observed at each generation as a function of the number of individuals measured and is non-accumulating. With time, the drift variance component dominates the overall variance of response. Nicholas (1980) has used the expressions for expected drift variance in response to develop some valuable graphs for size of experiment required either to obtain a specified coefficient of variation of response or to achieve a specified proportion of the expected responses to selection. Alternatively, if resources are limited, the expressions can be used to minimise the coefficient of variation of response as attempted by Soller and Genizi (1967) and Hill (1971). In this situation total population size would be fixed but there would be an optimum value for the proportion of the population selected as parents since reducing this proportion leads to both greater expected responses (through higher selection differential) and greater variance of response (through lower effective population size). Discussions of design of experiments for specific objectives are also available, for example:

- utilisation of information from relatives in single-trait selection(Hill, 1971).
- responses in correlated traits (Hill, 1971, 1978).
- experimental comparisons of alternative testing regimes (Hill, 1978).
- genetic assessment of potential indirect selection criteria (Hill, 1984a).

There are some specific aspects of design of selection experiments which have particular implications for sheep:

(i) Disproportionate selection of sexes
(ii) Overlapping generations
(iii) Control populations

(iii) Replication

(i) Disproportionate selection of sexes

In common with most farm animals, the numbers of males used for breeding in sheep is usually substantially fewer than the numbers of females. This led Hill (1971) to use effective population size to suitably weight the numbers of male and female parents used per generation.

(ii) Overlapping generations

Overlapping generations, represents a serious problem as it influences the basic assumptions made in estimating expected response, effective population size and expected variance of response:

Response. The usual simple expression for response to selection as a function of selection differential and heritability is only asymptotically true in a population with overlapping generations. However, Hill (1977) concluded that expected responses based on exact formulae accounting for the passage of genes throughout the population were never very different from the approximate expectations.

Effective population size. The concept of effective population size within a selection line across generations implies that the number of individuals entering the selection line each year and their parental age distribution remain constant. In the absence of maternal environmental effects due to age of dam, we would expect selection response to result in younger parents in the population being genetically superior and so increasing the probability of their progeny being selected in preference to the progeny of older parents. This should result in a shift in parental age distribution of selected individuals.

Variance of response. As in the case of expected responses to selection, the usual expression for drift variance is only asymptotically true for overlapping generations. Johnson (1977) has developed more exact formulae for this drift variance and shown the true drift in the early years of an experiment to be much larger than the apparent drift from the approximate formulae. Thus, the observations recorded in the first few years of an experiment are generally less reliable (or provide less information on genetic parameters) than would be first thought. In addition, since the generation interval usually consists of several time periods, or years, the importance of measurement error variance is relatively greater in relation to drift variance than in non-overlapping generations (Nicholas 1980).

(iii) Control population. A full discussion of the design of control populations can be found in Hill (1972c). Of particular interest here is the use of genetic information provided within the control and the population structure of this line.

In some past analyses of selection experiments, some information from the control has been used, particularly in calculating cumulative selection differentials in the control for the character under selection in the selected line (Pattie and Barlow, 1974; Blair and Pollak, 1984). Use of control line information in this manner implies that any directional selection operating in the control (presumably by chance) was applied to this one character alone and that the drift variance is reduced by this known selection. Such assumptions are probably unwarranted. Hill (1972c) described a situation of designed selection for zero selection differential in the control line where such reductions in drift variance can be validly claimed.

As mentioned previously the optimum proportion of the population selected as parents in a selection line involves a balance between the opposing factors of high selection differential and low genetic drift. For a control line, though, there is only the advantage of reducing genetic drift so that the proportion of the control line used as parents should be as high as possible. Since response is measured as a deviation of the selected line from the control and variance of response as the sum of the variances of the means for both selected and control lines, there are obvious advantages in minimising the expected variance in the control line. The control lines reported by both Pattie (1965) and Turner and Young (1969) in the Australian Merino experiments had larger numbers of males chosen each year than the selected lines.

(iv) Replication

The theoretical variance of response to selection represents the expected variance between conceptual replicated lines. In a replicated experiment, the variance of response can be estimated directly from the variance among replicates rather than based on some predictions of drift and measurement error (Hill, 1971). We shall see later that the analysis of an unreplicated selection experiment poses problems largely because the experiment does not provide an estimate of the true variance of response. The apparent error variance from an unreplicated experiment is usually biassed downwards and this bias increases with increasing heritability of the trait under selection and increasing duration of the experiment. In such an analysis, the expected variance of response can be predicted from the formulae developed by Hill (1971 et seq) but these predictions are based on some critical assumptions. In particular, it is assumed that the genetic and environmental variances and covariances remain constant in each population during the selection programme. Genes with large effects, inbreeding and linkage disequilibrium are some of the possible phenomena that could seriously disrupt such assumptions of constancy of variance. A comparison of expected between replicate variances with observed variances in replicated selection experiments with laboratory animals would be of great interest to those faced with an analysis of unreplicated selection experiments in domestic animals.

Thus, replication is of primary utility in providing a direct measure of the variance structure of observed responses to selection. Hill (1971) showed that if a population was divided into a number of subpopulations the variance of the mean selection response over all subpopulations is equal to that of the whole population as a single line. However, Nicholas (1981) has shown that the expected response across replicates is reduced from that expected in the total population as a single line because of the reduction in effective population size. For large effective population size and short-term duration of the experiment, this reduction in response can be kept below 10 per cent (Nicholas 1981). So replication per se should not seriously reduce the precision of the estimate of response to selection and does provide a valuable basis for statistical analysis.

ANALYSIS OF EXPERIMENTS

The most common form of analysis of selection experiments has been the regression of response on selection differentials. For direct response to selection, simple estimators of realised heritability by either the ratio of total response to total selection differential or the regression of cumulative responses on cumulative selection differentials each generation have been investigated by Hill (1971) and Hill (1972a,b) respectively. He recommended continued use of such estimators because they were generally highly efficient and unbiassed. Importantly, though, Hill (1972 a,b) showed that the common regression estimators of the variance of realised heritabilities from unreplicated selection experiments were substantially biassed downwards, and he suggested methods of improvement based on expected variances. It is critical that these expectations are based on several important assumptions and that an unreplicated experiment itself does not provide a direct measure of the most important component, the drift variance.

An alternative approach to analysis was used by Blair and Pollak (1984) who attempted separation of the genetic and environmental trends in a selected line using mixed model equations including the relationships between all animals. As a form of analysis in the absence of a control or a divergent selection line, there were two critical problems with the approach. Firstly, the 'realised heritability' or estimate of genetic trend was very dependent on the assumed prior heritability. Such a dependency would appear to reduce the value of selection experiments to little more than demonstrations of assumed genetic principles and parameters. Secondly, Blair and Pollak (1984) provided no evidence of any error structure within their method. Their assumed standard error was based on the formulae of Hill (1972b); arguments appropriate to standard least squares analyses. Thus, mixed-model methodology as an alternative to least squares for analysing selection experiments still requires some development. It may be, however, that the genetic structure within selected lines does provide some information on response (and its variance) additional to that provided by between line comparison, perhaps more so among populations with overlapping generations.

RESULTS OF EXPERIMENTS

A critical review of all selection experiments in sheep is an almost impossible task. Purser (1982) suggested that over 30 selection experiments had been commenced. Considering that Turner (1977) was able to list 23 such experiments in Australia with the Australian Merino breed alone and that this number did not include several other experiments known to the author, the actual number of sheep selection experiments throughout the world could be double Purser's estimate. The actual number is of no great importance except to indicate the lack of reported results from many of these experiments. Dalton and Baker (1980) have suggested that many studies have yielded little genetic information often because of poor design. Perhaps the results of some experiments indicated little response to selection or were difficult to relate to expected responses. Whatever the true explanation for this lack of reporting, the cost of selection experiments (in both human and physical resources) is so great that it is difficult to understand why such experiments have not been reported in more detail. It is also impossible to determine whether those experiments that have been published are a representative sample of all such experiments.

Direct responses to selection have been examined in published sheep selection experiments. These experiments can be grouped into three classes:

(i) The first group of experiments were single-trait selection lines which yielded an estimated realised heritability which would be compared with a base population estimate (Table 2.1). There are a number of general points that can be gleaned from this comparison of predicted and realised responses:

- the traits selected have been usually of moderate to high heritability.
- most of the experiments were of moderate duration of between 3 and 7 generations, thus giving quite precise estimates of realised heritability.
- the majority of realised heritability estimates have been

Table 2.1. A comparison of realised and base population heritability (h^2) estimates from single trait selection experiments in sheep.

Trait selected (breed)	Duration (years)	Realised h^2 (±s.e.)	Base population (±s.e.)	References (see below)
Fleece weight				
- Aust Merino	14	0.46±.05*(low) 0.24±.04*(high)	0.47±.07(O-D)**	7,4
- NZ Romney	21	0.23±.10(high)	0.31±.16(O-D)	1,10
- SA Merino	5	0.41±.08*	0.31±.07(PHS)	
Follicle Fleece				
- SA Merino	3	0.69±.12*	0.50±.14(PHS)	2
Crimp frequency				
- Aust Merino	14	0.46±.03*	0.47±.11(O-D)	11,4
Weaning weight				
- Aust Merino	10	0.25±.03*	0.18±.06(PHS)	6
- Cheviot	9	0.24±.11(high)	0.19±.09(PHS)	9
- crossbred (US)	3	0.22±.07*(high)	0.40±.17(PHS)	5
(2 locations)	3	0.18±.06*(high)	0.19±.08(PHS)	
Cannon bone length				
- Scottish Blackface	19	0.50±.03	0.54±.04(PHS)	8
Medullation index				
- Scottish Blackface	19	0.45±.03	0.48±.04(PHS)	8
Skin wrinkle				
- Aust Merino	19	0.36±.04	0.50±.07(O-D)	3,4

<u>References</u>: 1. Blair and Pollak (1974), 2. Heydenrych, Vosloo and Meissenheimer (1977), 3. McGuirk (1973), 4. Morley (1955), 5. Osman and Bradford (1965), 6. Pattie (1965), 7. Pattie and Barlow (1974), 8. Purser (1980), 9. Purser (1982), 10. Rae(1958), 11. Robards and Pattie(1967).

Direction of selection, either for high or low values of the trait. Where the direction is not specified the estimates were from divergent selected lines.

*Approximate standard errors estimated from published data using the formulae of Hill (1972a, b). For short-term experiments with overlapping generations (for example, Osman and Bradford (1965), these approximations are probably biassed downwards substantially.

**The method of heritability estimation is shown in parentheses; either offspring-dam regression (O-D) or paternal half-sib analysis of variance (PHS).

published with an inappropriate standard error because the analyses have ignored expected drift variance. In Table 2.1 some crude approximations based on the formulae of Hill (1972a, b) have been attempted from the published information on population structure and variance.

* generally, the estimate of realised heritability was slightly smaller and more precise than the base population estimate.

The experiment in which selection was practised for and against birthcoat score in Welsh Mountain sheep reported by Purser (1980) has not been included in Table 2.1. Response to selection in these lines was markedly asymmetric due to variance changes along the fixed range of scores. Realised heritability had a maximum value of 0.9 when the mean score was in the middle of the range but near either extreme was dramatically lower with a limiting value of zero.

There are a large number of single-trait selection experiments in which some response has been reported but for which selection differentials have not been published. In such cases it is not possible to compute realised heritabilities or, in many cases, to estimate the true variance of the observed responses. For example, Turner, Brooker and Dolling (1970) reported direct and correlated responses to selection in eight pairs of selected lines over 11 to 15 years of selection. However, applied selection differentials have not yet been reported for these lines.

(ii) Secondly, there are experiments from which an estimate of response has been obtained but for which no base population parameters are available. Land, Carr and Lee (1980) selected for and against a measure of testis size and observed a realised heritability of 0.4±0.08 from the divergent lines. The group of experiments aimed at increasing reproduction rate could also be classified into this group. These experiments, which were reviewed by Land, Atkins and Roberts (1982), all had slightly different aims although generally they were concerned with improving litter size. Observed responses are shown in Table 2.2. Predicted responses were based on average genetic parameters for litter size taken by the relevant authors from the literature and were typically 0.1 and 0.15 for heritability and repeatability respectively. Again, the correspondence between observed responses and, in this case, predicted responses from assumed (rather than estimated) base population parameters was very close. The trait under selection (litter size) had a low heritability but the average duration of the experiments was even longer than that reported for the single-trait experiments in Table 2.1. In addition, the effective population size of these lines was quite large.

(iii) The final group of experiments were generally multi-trait selection lines originally designed as a demonstration of selection response for some overall economic objective. Base population genetic parameters estimates have been used to develop a selection method which was then applied in a large population. An example is the report of Ercanbrack, Price and Terrill (1968) which gives observed responses in a number of traits from selection based on an index of economic merit. The interpretation of such responses in terms of realised genetic parameters is extremely

Table 2.2. Realised and predicted genetic responses in litter size of sheep.

Breed	Length of experiment (years)	Annual rate of response		Reference
		Realised	Predicted	
N.Z. Romney	13	0.018	0.021	Clarke (1972)
Galway	16	0.023	-	Hanrahan (1984)
Merino	14	0.02	-	Turner (1978)
Merino	10	0.018	0.015	Atkins (1980)
Merino	10	0.002	0.004	Mann, Taplin and Brady (1978)

difficult.

Three multi-trait selection experiments in the Australian Merino, where the principal criterion of selection was fleece weight, were reviewed by McGuirk (1980). Expected responses in fleece weight in all flocks was about two percent of the mean per year. In one flock the observed gain was one percent per year for 15 years (McGuirk 1980). In the other two flocks the responses were about two percent per year for the periods 1950-1959 (Turner, Dolling and Kennedy, 1968) and 1966-1974 (Turner and Jackson, 1978) while in the intervening period, gains previously achieved were not maintained (Turner, Dolling and Kennedy, 1968). The average rates of response over the 25 years of the experiment are not recorded but, presumably, they are substantially less than the expected rate of two percent per year.

Some factors influencing response

(i) Inbreeding and linkage disequilibrium

Inbreeding and linkage disequilibrium are two phenomena likely to result in a reduced rate of response to selection from that expected from unbiassed base population predictors of response. Increases in average inbreeding coefficient will result in a proportionate decline in the additive genetic variance of the trait under selection and thus a reduction in the realised heritability. In addition, the phenotypic expression of traits associated with fitness may be directly 'depressed' by moderate levels of inbreeding (see Lamberson and Thomas (1984) for a review of such effects in sheep). This inbreeding depression effect will only be of importance in experiments where selection responses are measured as the divergence between a selected line and a control and where the two lines have markedly different rates of inbreeding increase. Linkage disequilibrium effects on selection response have been studied extensively. If the base population from which a selection experiment is commenced is in linkage equilibrium for the trait to be selected, the expected heritability after selection can be computed from the approximate formulae given by Bulmer (1980). As a simplification, with the typical selection pressures applied in sheep populations, the realised heritability of a trait might be expected to be about 90 percent of its base population (linkage equilibrium) value. This reduction can be expected within the first few rounds of selection and quickly stabilise, although it is likely that overlapping generations will delay this approach to stability.

Whilst inbreeding can reduce expected responses to selection, the avoidance of inbreeding can also reduce response. A rather extreme example of avoidance of inbreeding would be selection within sire families. Compared with mass selection, within sire family selection results in a decrease in the potential selection differential and the heritability of the trait (Falconer, 1981). The size of the decrease depends on the family size and the true heritability but is commonly about 25 percent. Purser (1980) reported selection responses from experiments in which within sire family selection was assumed to be operating. Less extreme forms of inbreeding avoidance have also been used in some selection experiments but expected effects on selection response have not been pursued.

(ii) Scale effects

Scale effects are most frequently observed as asymmetric responses to selection in divergent lines. Such asymmetry is often due to the distribution of the trait being non-normal such that the variance alters with the mean, for example the responses in birth coat score observed by Purser (1980). Other examples of scale effects in sheep selection include the medullation lines of Purser (1980) for which a simple transformation apparently produced normality, and the fleece rot lines of McGuirk et al (1978) in which the character under selection is a binomially distributed trait. Perhaps less obviously, the lines selected for litter size all involve some scale effects. The upward selected lines of Clarke (1972) and Turner (1978) both had a contemporaneous downward selected line in which responses were very small since selection was towards the observable limit of the trait. The importance of such scale effects on the estimates and interpretation of the responses to selection for litter size is not clear.

(iii) Genotype x environment interactions

An experiment designed to estimate genotype x location interactions in weaning weight was established by Osman and Bradford (1965) but continued for a relatively short time period with no evidence of substantial interaction (Table 2.1). A longer experiment has been conducted in Australian Merinos with fleece weight as the selection criterion (Turner, 1977) but the results have not yet been reported.

McGuirk (1980) has reviewed evidence of genotype x plane of nutrition interaction for fleece weight in the Australian Merino.

The superiority in fleece weight of lines selected for high fleece weight over control lines increased with increasing feed intake among pen-fed sheep (Saville and Robards, 1972; Piper and Dolling, 1969). Similarly, the superiority of the high fleece weight line at pasture was positively related to the level of performance of a control or low fleece weight group with which they were compared (Hamilton and Langlands, 1969). McGuirk (1980) implied that the apparent asymmetry in response to selection for fleece weight in the experiment of Pattie and Barlow (1974) (see Table 2.1) could be due to this genotype x nutrition interaction.

(iv) Maternal effects

From Table 2.1, the character most likely to show maternal environmental and maternal genetic effects was weaning weight. The results of Pattie (1965) show a higher heritability from offspring-dam regression than that from paternal half sib analysis with the realised heritability intermediate. This result is the expected pattern for a trait with maternal genetic influence since the expected composition of the various heritability estimators in terms of additive direct (σ^2_O), additive maternal (σ^2_M) and total phenotypic (σ^2_P) variances are:-

paternal half sib $h^2 = \sigma^2_O/\sigma^2_P$
offspring-dam $h^2 = (\sigma^2_O + \sigma^2_M)/\sigma^2_P$
realised (mass selection) $h^2 = (\sigma^2_O + 1/2\sigma^2_M)/\sigma^2_P$

Using cross-fostering techniques, Yates and Pattie (1970) attempted to separate post-natal maternal effects from direct genetic effects and, with limited precision, concluded that the total response in increasing weight was about equally derived from response in direct and maternal genetic effects. The maternal response involved was apparently total milk production of the ewe (Pattie and Trimmer, 1964).

The pattern of response in direct and maternal components of a trait under selection has been examined by Mueller (1983). He showed that in a population with overlapping generations the total response and the relative contribution of the components of this response can be quite irregular in the early years of an experiment and, in particular, maternal genetic response may be slow in reaching its asymptotic rate.

(v) Genes of large effect

An example of genes of large effect influencing selection response can be seen from the report of Turner (1978) in which the responses of two lines selected for increased litter size were compared. The first line (shown in Table 2.2) had an expected rate of response while the annual response in the second line (Booroola flock) was at least five (5) times greater than expected. Piper and Bindon (1982) subsequently demonstrated that a gene with a major influence on litter size and ovulation rate was apparently segregating in this Booroola line. The period of responses examined by Turner (1978) probably represented a large increase in the frequency of this gene.

CONCLUSIONS

Some selection experiments have produced an impressive amount of information on the genetic improvement of some traits. One could point to the selection experiments in Australian Merinos for fleece characters which have increased our ability to develop relevant breeding plans. In addition, they have increased our understanding of the genetic control of wool biology as evidenced by the studies of physiological responses to selection reviewed by McGuirk (1980). Alternatively, the long-term experiments reported by Clarke (1972) and Turner (1977) on responses to selection for increased litter size have, arguably, contributed more to the incorporation of litter size as a selection objective into sheep improvement programmes than base population heritability estimates. These two groups of experiments were distinguished by several features:-

* selected lines were replicated, across locations admittedly, but the perceived precision of the responses was that much greater.
* the lines were maintained for 20 or more years so that the observed responses were quite large.
* having obtained a measurable difference between selected lines, experimental comparisons were used to examine such issues as correlated changes in expensive to measure characters (for example, feed efficiency, wool manufacturing ability), biochemical and physiological components of response, and genotype x environment interactions.

In many respects these features encapsulate both the advantages and limitations of selection experiment design. Selection experiments can yield relatively precise estimates of response to selection and generate distinct lines that can provide information on biological variation and control. However, the experiment needs to be well-designed which usually requires a commitment of large physical resources in terms of population sizes and a moderately long period of time. Several of the sheep selection experiments reviewed here were maintained for such a short time period or had such small effective population sizes that their scientific value was dubious. The general principles of design have now been well documented by Hill (1971 et seq) although some additional aspects have been considered here.

Another important conclusion from many sheep selection studies has been the inadequate statistical analysis of the observed responses. The published sampling variance of realised heritabilities were, in many cases, incorrectly estimated since genetic drift was not appropriately accounted for (see Table 2.1). Although improved methods have been suggested in the literature, there is a need for these to be developed and applied. Additionally, extension of improved methods to populations with overlapping generations needs to be investigated.

CHAPTER 3

DESCRIPTION OF EXPERIMENTAL METHODS

AIMS OF THE EXPERIMENT

The original aims of the experiment must first be placed within an historical perspective. The experiment was designed in the mid-1950'S at a time when single trait selection lines were not common in farm animals and some of the classical selection experiments in mice and Drosophila were just commencing. It was planned that the experiment should continue for a sufficiently long period to generate large differences between divergent lines. Given the average generation interval in domestic sheep, it was appreciated that an experiment of 8-10 generations would take 20-30 years to complete. The objective of the programme was to provide an experimental check on the validity of predicting selection responses from quantitative theory. That such an experimental validation was seen to be required may seem of doubtful interest today but that is only because of our acquired experimental knowledge since that time. In fact, the classical experiment in Drosphila reported after the start of this experiment by Clayton, Morris and Robertson (1957), had precisely the same aim. What may be more arguable is that such an experimental check was required in domestic animals, or sheep in particular, given that such information was being collected in laboratory animals, especially the mouse. Such hindsight, though, should continue to remind us of the basic limitations of selection experiments in many domestic species, that suitably precise results take a long time to be realised. Thus, the justification for commencing a selection experiment in such species must be powerful and the experiment must have precise aims.

The specific historical objectives of this experiment as described in the Annual Reports of the Animal Breeding Research Organisation (1954-56), were threefold: (i) To measure direct and correlated responses to selection and compare such responses with those predicted from base population parameter estimates.

(ii) To determine whether directional selection for a single trait caused undesirable changes in any fitness component. It was assumed, perhaps, that the population was at an optimum for fitness and that any long-term selection in any direction may induce a decline in fitness.

(iii) To produce selected lines that were markedly different from each other that could be used for physiological studies and might give some clue to the derivation of some of the large differences apparent amongst modern sheep breeds.

The actual traits for selection were chosen after considering the following issues which affect likely rates of response (Purser, 1967):

(a) The traits should be easily and quickly measurable with a high repeatability and a high heritability.

(b) The traits could be measured in young animals so that the largest possible numbers were available for selection and generation interval could be kept as short as possible.

(c) The traits should be correlated with characters of economic importance in order to generate divergence in these characters and so have some relevance to practical sheep breeding.

The traits chosen were cannon bone length and medullation index. Cannon bone length was intended as a useful measure of carcase conformation. Short cannon bone length was considered typical of Down-type breeds producing desirable carcases with fast rates of maturity while long cannon bone length was more typical of wool breeds producing poorer carcases with relatively slow rates of maturity. Since it was intended to change conformation per se, expected correlated responses in body weight were to be controlled by adjusting the bone length measurement for the positive phenotypic regression of cannon bone length on body weight in the hope that genetic changes in body weight would be zero. Selection on medullation index was intended to produce differences in wool quality typified by breed differences between carpet-wool and fine-wool breeds.

Against this historical perspective, what can an analysis of selection resposnes in this experiment contribute to our current knowledge of sheep genetics? We are concerned here with the lines selected for high and low cannon bone length adjusted for body weight differences. The specific aims of this report are:

(1) Comparison of realised direct and correlated responses to selection with predicted responses from base population parameter estimates. It has already been shown in Chapter 2 that, despite the relatively large number of selection experiments in sheep, few

have been satisfactorily reported in terms of realised heritabilities and genetic correlations. This experiment was probably the largest sheep experiment so far conducted in terms of annual size of the breeding flock and duration in generations, and so it is admirably suited to such an analysis.

(ii) Examine the effect of selection in producing changes in parameters. This question is of particular interest in that the selection trait was an index and so we are interested in the genetic and phenotypic parameters of the index and the two component traits.

(iii) Traditionally, conformation has always been viewed as an important production trait of sheep both in its effect on price received for lamb carcases and as a selection objective. Geneticists have generally tried to caution against 'wasting' selection effort on conformation but little objective data has been available on which to base such a judgement or use as evidence for such advice. This experiment should provide evidence for the likely changes in characters of economic importance when selection is based on a measure of conformation.

EXPERIMENTAL DESIGN AND MANAGEMENT

General design

In 1951, a flock of approximately 1600 mixed age Scottish Blackface ewes was assembled on the Animal Breeding Research Organisation's hill farm at Stanhope, Peeblesshire in Scotland. The farm is located in the upper Tweed valley and comprises about 2500 ha of unimproved heather-based hill land and about 50 ha of lowground enclosed fields. The hill land consisted of four distinct but largely unfenced regions, called hirsels. Ewes introduced to a particular hirsel then remained in that region for their entire life. In addition, however, groups of ewes congregated within specific areas of a hirsel and tended to graze exclusively within these narrow territories, or hefts. For example, some ewes would always be found on the lower slopes of the hill while others, almost exclusively grazed the upper slopes. The four hirsels each carried approximately equal numbers of permanently hefted ewes.

The original flock was managed as a random breeding unit between 1952 and 1955 inclusive. Rams were purchased and were used repeatedly to sire offspring born in 1952, 1953 and 1954. Pedigrees and recorded traits on lambs born in 1952 and 1953 were incomplete and so it was decided to restrict data analysis to lambs born from 1954 onwards. Lambs born in 1954 and 1955 are subsequently referred to as the BASE flock.

Prior to mating in November 1955, the 1600 ewe flock was randomly subdivided into six (6) lines of equal size across hirsels. One of these lines (RANDOM) was selected at random but managed separately from the other flocks. This flock was group-mated to a relatively large number of rams and so sire identity of any lamb born was unkwnown. Data from this flock have not been considered. The remaining five lines were managed as a single experimental group except at mating and were designated as follows:

CONTROL - selected randomly

LONG - selected for long cannon bone length

SHORT - selected for short cannon bone length

HAIRY - selected for high fibre medullation

FINE - selected for low fibre medullation

The selection criterion in the LONG and SHORT flocks was cannon bone length measured at 8 weeks of age and adjusted for the phenotypic regression with body weight measured at the same age. The form of adjustment was standardised throughout the experiment as:

$$\underset{(cm)}{COR} = \underset{(cm)}{CBL} - 0.176\,(\underset{(kg)}{WT} - 13.6)$$

where COR = adjusted cannon bone length
CBL = cannon bone length at 8 weeks of age
WT = body weight at 8 weeks of age

The origin of this adjustment was described by Purser (1960). The aim of the index was to both increase the efficiency of selection and to restrict genetic change in body weight. Although the estimated regression required for zero genetic response in WT was higher than 0.176, the genetic covariance estimate between CBL and WT was imprecise and so the phenotypic regresson estimate was used (Purser 1960).

The size of the ewe flock of each line was maintained at approximately 270 ewes for the duration of the experiment from 1955 to its conclusion in 1974. Ewes first entered the flock for mating at 18 months of age and, subject to any wastage due to death or necessary culling, remained in the flock for five annual matings such that they were culled for age at 6 years. All ewes were inspected prior to mating each year and any ewe considered incapable of rearing a lamb in the ensuing year was culled. The major culling criteria were skeletal faults, udder abnormalities and broken mouths. The ewes in each line were mated at random, but in equal numbers, to 10 young sires (7 months old) in each year.

Selection of replacement ewes and rams

In 1955, all available ewe and ram lambs were assigned to breeding lines at random and selections were made within these newly created breeding lines on the basis of the appropriate selection criterion. From 1956, lambs belonged to their parental breeding group and selections were limited to these closed lines.

There was an initial culling of ewes and rams by the farm shepherds on some form of visual assessment. Lambs with physical faults and abnormalities (such as bad legs, mouths etc) were not considered for selection. Additionally, animals of small size and weight were not considered, primarily because selected rams were expected to be capable of mating ewes at 7 months of age. Between 15 and 25 percent of available animals were rejected on these characters each year.

Selection in each line according to the selection criterion appropriate to that line was then practised amongst the visually acceptable lambs.

Amongst ewes, very little selection on the appropriate criterion was actually applied since visual culling reduced ewe numbers to almost those required to maintain flock size. On average, 65 ewes (18 months of age) entered each breeding line each year.

As already stated, 10 sires were used in each line in each year. At 8 weeks of age, 17 to 20 rams were initially chosen and, of those surviving, a final selection of 10 rams was made immediately prior to mating at 7 months of age. Apart from the visual culling, selection of rams was based on the estimated phenotypic selection differential for the trait under selection in each line. In addition, the parentage of each ram was considered in an attempt to reduce the rate of increase in inbreeding. The restrictions on rams selected at 8 weeks of age were:

(i) No ram lamb could be selected whose dam had already had a ram lamb chosen and used for breeding in a previous generation.
(ii) As far as possible with the lambs available, at least one (1) and no more than (3) ram lambs were to be chosen from the offspring of each sire and grandsire.

Management and records

(i) Lambing to weaning

Lambing commenced at about the beginning of April each year. Up until 1967 all ewes lambed on the hill while subsequently all ewes lambed on the lowground and immediately after lambing were returned to the hill. Shortly after birth each lamb was identified with its dam, eartagged and weighed. For any ewe considered incapable of rearing her lambs, a suitable replacement ewe was sought and lambs were fostered when such a replacement dam was available. For about five percent of all live lambs born fostering was attempted. Any ewe rearing two lambs was pastured on the lowground fields shortly after lambing and remained there with her lambs for at least two and up to four months.

Lambs remained undisturbed with their dams until the average age of the lambs was about eight weeks. All lambs were then gathered and measurements of body weight, cannon bone length and medullation index were recorded. Cannon bone length and medullation index were measured separately by two independent observers and an average calculated. At this time, preliminary selection of rams and ewes were made as described previously. Any ram lamb not chosen as a potential sire was castrated. All ewes and lambs were then returned to their appropriate hirsel, although, in some years, ewes rearing twin lambs were returned to the lowground fields.

The lambs were weaned from their dams in August at approximately four months of age. All lambs were weighed. Unselected ewe lambs, all castrated males (wethers) and all crossbred lambs from chaser rams were separated from the remaining lambs and managed separately until disposal.

(ii) Weaning to hogget

Ram lambs from all lines were managed as a single flock on the lowground until required for mating at 7 months of age.

The selected ewe lambs were returned to their appropriate hirsel on the hill and were weighed again in October when they were six months old. The management of ewe lambs over their first winter varied between years. For lambs born between 1954 and 1959, 60 to 70 percent of all ewe lambs were grazed at other farms on lowground pasture between November and March. The remaining ewes grazed on their hirsel of birth on the hill. This practice of away-wintering has been assessed as a management strategy by Purser and Roberts (1964). Ewe lambs born between 1960 and 1968 were all returned to the hill for their first winter while those born after 1968 were grazed on the lowground fields at Stanhope from late December until the commencement of lambing.

The ewes were weighed at 12, 14 and 16 months of age in April, June and August respectively. Ewes wintered away had all returned to Stanhope by the April weighing. At the time of the June gathering (14 months of age), the ewes were shorn for the first time and fleece weight record ed. In addition, the cannon bone length was again recorded at 14 months of age.

(iii) Adult ewes

Prior to mating, ewes were gathered from the hill, weighed and allocated to individual sires at random within age groups. The single-sire mating groups of about 27 ewes each were enclosed in separate lowground fields and ewes remained in their allocated groups until the end of mating. The mating period commenced in mid-November and continued for about 30 to 35 days, allowing two oestrous cycles for all ewes. Rams were fitted with raddle harnesses to allow identification of ewes served by the rams. Any ram not working satisfactorily after the first two weeks of mating was replaced by a reserve ram from the same selection line.

At the end of the mating period, white-faced rams (mainly

Welsh Mountain or Cheviot) were introduced to the ewes for about two weeks. White-faced rams were used so that any progeny resulting from these chaser matings would be clearly colour-marked. All adult ewes were then returned to the hill and remained there throughout pregnancy, although supplementary feeding was offered for the final six weeks of pregnancy. Up till 1960, this supplementary feeding was in the form of hay but subsequently also included some protein concentrate.

Lambing, and management of the ewes to weaning have already been described. Adult ewes were shorn annually in July shortly before their progeny were weaned. After weaning, all ewes returned to the hill until mating.

STATISTICAL ANALYSIS

There were two major thrusts to the statistical analyses of the data: namely, estimation of genetic parameters in the unselected populations (BASE and CONTROL) and estimation of realised responses to selection in the selected populations (LONG and SHORT). The general procedure followed is presented here while specific details of all analyses are described in each experimental chapter.

Estimation of genetic parameters

Each trait was analysed by least squares analysis of variance using the LSMLGP program (Harvey 1977). Initially the significance of certain fixed effects was tested against the within-sire error variance. Since the sires were completely nested within years, sires (and hence years) were absorbed and the fixed effects fitted within this absorbed model. The fixed effects tested were:

* hirsel. There were four hirsels representing distinct areas of the farm.
* birth/rearing type. The classifications were born and reared as singles, born as twins but reared as singles and born and reared as twins.
* ewe age. The age of the dam at the time of her progeny's birth which could be 2,3,4,5 or 6 years of age. This variable was fitted as a main effect with five discrete levels.
* birth date. Since all measurements between years were timed from the commencement of lambing, date of birth completely described an animal's age. Birth date was fitted as a continuous variable (or covariate) and (birth date)^2 was also fitted to test non-linear relationships.

In addition, various first-order interactions between the fixed effects and between year of birth and the fixed effects were fitted. For records measured after six months of age a further fixed effect for first winter treatment was also fitted since some animals in some years were wintered away from the hill. Interactions and main effects that were not significant ($P>0.05$) sources of variation were successively omitted from the model and the reduced models refitted until an appropriate model was determined for each trait.

Having established a suitable model for the fixed effects, a mixed model was then fitted with year of birth as a fixed effect, sires nested within years as a random effect and then the other fixed effects as previously determined. The variance component for sires was calculated and heritability estimated as:

$h^2 = 4\sigma^2 s / (\sigma^2 s + \sigma^2 w)$

where h^2 = heritability

$\sigma^2 s$ = between-sire variance component

$\sigma^2 w$ = within-sire variance component

The standard error of the heritability was estimated using the formula for the standard error of an intra-class correlation as described by Becker (1975).

The data for each individual trait were first adjusted for significant fixed effects (excluding year of birth) before genetic correlation analyses were undertaken. This was done because the data set was not complete for all traits and because different fixed effects were of importance for different traits. Therefore, rather than explicitly fitting all fixed effects in each analysis, each trait was first adjusted for the important effects appropriate to that trait from the whole data set, and all subsequent analyses performed on the adjusted data. Genetic correlations were estimated between pairs of traits and all animals with observations for both traits were included. The model contained year of birth and sires nested within year. Variance components for between- and within-sires were calculated and genetic and phenotypic correlarions were estimated from:

$r_g = \sigma s_{12} / (\sigma^2 s_1 \, . \, \sigma^2 s_2)^{1/2}$

$r_p = (\sigma s_{12} + \sigma w_{12}) / [(\sigma^2 s_1 + \sigma^2 w_1)(\sigma^2 s_2 + \sigma^2 w_2)]^{1/2}$

where r_g = genetic correlation

r_p = phenotypic correlation

$\sigma^2 s_i$ = between-sire component for trait i (i=1,2)

$\sigma^2 w_i$ = within-sire variance component for trait i

σs_{12} = between-sire covariance for traits 1 and 2

σw_{12} = within-sire covariance for traits 1 and 2

The standard errors of the correlations were estimated as a linear function of the observed variances and covariances as described in detail by Becker (1975).

Estimation of responses to selection

The selection applied in each line was estimated by the average cumulative selection differential of all lambs born in a line in a particular year. Since the progeny of ewes could be born in different years, a procedure to combine information across years was required ans the following method was used. Cumulative, individual and total selection differentials for adjusted cannon bone length (COR) were estimated for all animals in the CONTROL, LONG and SHORT lines. For each lamb born, the cumulative selection differential was calculated as the average of the total selection differentials of its parents. An individual selection differential for each lamb was calculated as the deviation of its own COR measurement from the mean COR of all lambs of the same sex born in the same year in the same selection line. The total selection differential appropriate to an animal then arises from the sum of the average cumulative selection differential of all lambs born of the same sex in the same year in the same selection line and the individual selection differential which measures the phenotypic deviation of the animal from this contemporary group. For all ewes in the BASE flock born prior to 1954 (for which there were no COR measurements available), the total selection differentials were assumed to be zero.

This method of computing selection differentials is similar to that used by Pattie (1965) and described by Turner and Young (1969) except for estimating total selection differentials. Pattie (1965) estimated total selection differential for an individual as the sum of the individual selection differential and the average of the total selection differentials of its parents. Since an above-average individual will tend to have above-average parents the effect of the Pattie (1965) method is to double count the superiority of an individual by including both its mean parental deviation and its own phenotypic deviation from its contemporary group. The incorrect method has been used extensively in the analysis of sheep selection experiments. The error of the method was pointed out to me by J.W. James (personal communication), although Newman, Rahnefeld and Fredeen (1973) used an appropriate method for cumulating selection differentials in a cattle selection experiment. The effect of the incorrect method on the estimated cumulative divergent selection differentials in each year can be seen from Table 3.1. After the first year of the experiment the incorrect method overestimated the true selection differential in each line increasing up to 15-20 percent above the true value. Clearly, the use of the Pattie (1965) method of cumulating selection differentials will substantially overestimate them and thus underestimate realised heritability.

Table 3.1. Cumulative selection differentials for COR (cm) as estimated by (i) the correct method and (ii) a commonly used, incorrect method first suggested by Pattie (1965). The selection differentials represent the divergence between the LONG and SHORT lines.

Year of birth	Selection differential for COR (cm) by:-	
	(i) correct method	(ii) incorrect method
1956	0.62	0.62
57	0.80	0.84
58	0.99	1.06
59	1.09	1.15
60	1.37	1.48
61	1.76	1.99
62	1.90	2.23
63	2.17	2.46
64	2.36	2.71
65	2.68	3.11
66	2.88	3.41
67	3.06	3.54
68	3.26	3.80
69	3.54	4.15
70	3.81	4.50
71	4.13	4.92
72	4.29	5.13
73	4.43	5.35
74	4.69	5.57

Cumulative direct response to selection in each year was calculated for the LONG and SHORT lines as the difference between the mean COR in each line and the mean COR in the CONTROL line. The regression of cumulative responses on average cumulative selection differentials was then estimated separately for the LONG and SHORT lines. These regressions where forced through the origin since all lines were derived from the same base population. Where differences between the regressions from each selection line were not significant, the CONTROL line was ignored and the regression estimated from the divergence between the LONG and SHORT lines in each year for both cumulative selection differentials and response. Cumulative correlated responses to selection and the regressions of cumulative correlated response on cumulative selection differential (for COR) were estimated in the same manner as that described for direct responses. An exception to this method occured with binomially distributed correlated traits and the methods used will be described where appropriate.

Hill (1972a) showed that the variance of an unweighted regression of response on selection differential is biassed downwards since the individual year observations are treated as independent whereas they are correlated with each other due to genetic drift. The variances of direct and correlated responses appropriate for an unreplicated selection experiment with observations at discrete generations were developed by Hill (1971). Johnson (1977) showed that the asymptotic rate of drift accumulation was an underestimate of the actual rate of drift in the early years of a selection line with overlapping generations. Using the approach of Hill (1971) and the modification of Johnson (1977), the expected variance-covariance matrices of responses to selection in each year of this experiment were derived. A generalised least-squares solution for the regression of response on selection differential was possible, with an appropriate variance, from:

$$B = (X' V^{-1} X)^{-1} \; X' V^{-1} Y$$

where

B = regression coefficient of ccumulative response on cumulative selection differential
X = vector of cumulative selection differentials
Y = vector of cumulative responses
V = variance-covariance matrix of cumulative responses

Details of the formulation used to generate the variance-covariance matrices for both direct and correlated responses will be decribed in the experimental chapters.

In a situation of mass selection, the regression of direct response on selection differential is an estimate of the ratio of additive genetic variance on phenotypic variance, that is, realised heritability. The regression of correlated response on selection differential estimates the ratio of additive genetic covariance between the directr and correlated traits on phenotypic variance for the direct trait, or:

$$b = r_G h_1 h_2 \sigma_2 / \sigma_1$$

where r_G = genetic correlation
$h^2{}_1$ = heritability of selected trait

h^2_2 = heritability of correlated trait

σ^2_1 = phenotypic variance of selected trait

σ^2_2 = phenotypic variance of correlated trait

Using this equation and estimated values for the other parameters, estimates of realised genetic correlations were obtained.

CHAPTER 4

CANNON BONE LENGTH, BODY WEIGHT AND A DERIVED INDEX BETWEEN THE TWO TRAITS:

GENETIC AND ENVIRONMENTAL SOURCES OF VARIATION

INTRODUCTION

This chapter reports the sources of variation, both genetic and environmental, affecting cannon bone length and body weight at eight weeks of age. The data consisted of animals born between 1954 and 1974 inclusive in an unselected control flock. In 1956, selection lines were commenced for high and low cannon bone length adjusted for body weight by a fixed linear function. Estimated genetic and environmental effects for this index are also presented. Subsequent chapters will report base population estimates of genetic correlations and realised direct and correlated responses to selection for cannon bone length adjusted for body weight.

MATERIALS AND METHODS

A description of the location and environment, and the sheep and their routine management has been presented in Chapter 3.

Measurements

Cannon bone length (CBL) and body weight (WT) were measured on each lamb at one time each year, when the average age of all lambs was approximately eight weeks. Cannon bone length adjusted for body weight (COR) was estimated for each animal using a standard linear adjustment. Selection lines, which are described in detail in a subsequent paper, were established in 1956 using COR as the selection criterion. The form of adjustment was:-

$$\underset{(\mathrm{cm})}{\mathrm{COR}} = \underset{(\mathrm{cm})}{\mathrm{CBL}} + 0.176\,(13.6 - \underset{(\mathrm{kg})}{\mathrm{WT}})$$

This form of adjustment was derived from an analysis of the base flock in 1954-55 which estimated the phenotypic regression of CBL on WT (0.176cm/kg) and the mean WT (13.6kg or 30 lb).

The data reported in this chapter represent the base population (1954-1955) and the unselected control flock (1956-1974). The number of animals included in the analyses is shown in Table 4.1.

Statistical analysis

(i) Fixed environmental effects

Least squares analysis of variance were performed on CBL, WT and COR to estimate the effects of year of birth, sires within years, hirsel, sex (rams and ewes), birth/rearing type (singles, born twin-raised single, and born and raised as twins), ewe age (2, 3, 4, 5 and 6 years of age), birth date and (birth date)^2; the latter two effects being fitted as covariates. In addition, various first-order interactions between the fixed effects and year of birth, and between the fixed effects themselves were fitted. Non-significant ($P>0.05$) interactions were progressively omitted from the analyses and the reduced models refitted. In fact, no interaction approached significance for any of the traits.

The trait COR was computed throughout the experiment using the fixed linear adjustment of CBL for deviation in WT described previously. Further analysis of CBL was performed using a similar model to that described above but also introducing WT and (WT)^2 as covariates. This model was used to determine the consequences of using the fixed adjustment compared with, retrospectively, the best

Table 4.1. Numbers of sire groups and lambs according to year of birth

Year born	Sires	Lambs
1954	35	512
1955	61	565
1956	12	192
1957	11	227
1958	11	202
1959	10	242
1960	11	197
1961	10	200
1962	10	188
1963	11	196
1964	11	174
1965	10	195
1966	11	167
1967	10	190
1968	10	202
1969	10	196
1970	10	197
1971	11	207
1972	10	186
1973	10	221
1974	11	211
Totals	296	4867

adjustment available.

(ii) Genetic and environmental sources of variation

Measurements of CBL and WT were recorded on lambs at eight weeks of age which was about midway between birth and weaning. The possibility of maternal genetic and environmental influences on such traits was clearly relevant. A number of different estimators of heritability were obtained from the data set. The approach was then to set these estimators equal to their expectations in an attempt to estimate the casual components of variance. The estimators used and their expectations are set out in Table 4.2. The expectations for the genetic components were arrived at by the use of Willham's (1963) formula:

$$\mathrm{Cov(Px,Py)} = \mathrm{Rxy}\,\sigma^2\mathrm{Ao} + \mathrm{Rwz}\,\sigma^2\mathrm{Am} + \mathrm{(Rxz{+}Rwy)}\,\sigma\mathrm{AoAm} + \mathrm{Vxy}\,\sigma^2\mathrm{Do} + \mathrm{Vwz}\,\sigma^2\,\mathrm{Dm} + \mathrm{(Vxz{+}Vwy)}\,\sigma\mathrm{DoDm}$$

where x and y are individuals, and w and z contribute the maternal components to x and y respectively.

Cov (Px,Py) = covariance between phenotypes of x and y

Rxy = Wright's coefficient of relationship between x and y

Vxy = probability that both genes at a locus in x are identical by descent with the two genes at that locus in y.

σ^2Ao = additive genetic variance for direct effects

σ^2Am = additive genetic variance for maternal effects

σ^2Do = dominance variance for direct effects

σ^2Dm = dominance variance for maternal effects

Table 4.2. Estimators of heritability and their expectations

Model type	Estimator+	Expectations*				
		σ^2_{Ao}	σ^2_{Am}	σ_{AoAm}	$(\sigma^2_{Em}+\sigma^2_{Do})$	$(\sigma_{EoEm}+\sigma_{DoDm})$
Paternal half sib (PHS)	$4\sigma^2_s/\sigma^2_p$	1				
Offspring-sire (O-S)	$2b_{os}$	1		0.5		
Sire's offspring and grand-progeny (MGS [O-GP]	$8b_{og}$	1		2		
Offspring-maternal granddam (O-MGD)	$4b_{oG}$	1	1	2.5		
Grandmaternal sire's quarter-sibs (GMSQS)	$4\sigma^2_s/\sigma^2_p$	0.25	1	1		
Offspring-dam (O-D)	$2b_{od}$	1	1	2.5		2
Maternal half sib (MHS)	σ^2_d/σ^2_p	0.25	1	1	1	

*$\sigma^2_{Ao}(A_m)$ = additive genetic variance for direct (maternal effects)

$\sigma^2_{Do}(D_m)$ = dominance variance for direct (maternal) effects

σ^2_{Em} = environmental variance for maternal effects

$\sigma A_oA_m(D_oD_m)$ = covariance of additive (dominance) direct and maternal effects

σE_oE_m = covariance between maternal and direct environmental effects

+σ^2_p = phenotypic variance

σ^2 = variance component; s = sires, d = dams

b = regression coefficient between relatives; OS = offspring-sire; Og = offspring-grandprogeny; OG = offspring-granddam; Od = offspring-dam

σ^2AoAm = covariance of additive direct and maternal effects

σ^2DoDm = covariance of dominance direct and maternal effects

Statistical models

The records for each lamb were first adjusted for the fixed effects of ewe age, birth type and birth date, and all analyses were then performed on these adjusted records. The analyses were done within sex (due to variance differences) and subsequently pooled estimates across sex were obtained, provided sex differences in the estimates were not significant.

There were two categories of animal that could affect the expectation of the estimates; namely, fostered lambs and full sibs (of like sex only since the analyses were done within sex). A total of 150 lambs were raised by foster dams. Where the expectation of the heritability estimate contained an additive genetic maternal component (O-D, O-MGD, MHS and GMSQS), all fostered lambs were deleted from the data prior to analysis. Similarly, where the heritability expectation was derived from variance components between collateral relatives (PHS, MHS and GMSQS), one of each pair of like-sex full sibs was randomly deleted from the data. A total of 147 animals were deleted for this reason.

The statistical models used for the analyses are summarised in Table 4.3, together with the appropriate data deletions. The computer program LSML76 (Harvey, 1977) was used for all analyses. Standard errors were calculated according to Latter and Robertson (1960) for regression estimators and Becker (1975) for variance component estimates. Genetic, phenotypic and environmental

Table 4.3. Statistical models for estimating heritability

Estimate type	Data excluded		Nesting of records
	Full-sibs	Fosters	
PHS	x		Offspring/sires/year$^+$
O-S			Offspring and sire/year
MGS [O-GP]			Grand progeny and offspring/year (offspring)
O-MG		x	Offspring and granddam/year (offspring)/year (granddam)
GMSQS	x	x	Offspring/dams/maternal grandsires/year
O-D		x	Offspring and dam/year (offspring)/year (dam)
MHS	x	x	Offspring/dams/year

* See table 4.2 for explanation of abbreviations

$^+$ year refers to the year of birth of the group included in parentheses. Since sires were used once only throughout the experiment, year of birth of sires also specifies the year of birth of their offspring.

correlations between CBL, WT and COR were also estimated from these analyses.

Estimation of components

From Table 4.2, there were five unknown parameters and seven equations. Solutions for the five parameters values were obtained by a least-squares procedure suggested by Eisen (1967). Each equation was weighted by the inverse of the sampling variance of the heritability estimate and least-squares means for each component and a standard error were obtained. Since all the components estimated in this way were proportions of the phenotypic variance, the direct environmental component was estimated as the difference between unity and the sum of the individual components (excluding direct-maternal environmental covariance which is not expressed in the phenotype of an individual).

RESULTS

(i) Environmental fixed effects

The analyses of variance for CBL, WT and COR are summarised in Table 4.4. Hirsel, ewe age, sex and birth type had significant influences on all characters. Birth date, too, accounted for a significant proportion of the total variance showing a curved relationship with CBL and COR, but no evidence of curvilinearity with respect to WT. The effect of the linear adjustment of CBL for WT (COR) was to substantially reduce between-year variation, the error variance and the amount of variation accounted for by the fixed effects. The reduction in sums of squares due to fitting ewe age, sex, birth type and birth data within sire subclasses was 17.2%

Table 4.4. Summary of analyses of variance

Source of variation	d.f.	Mean squares			
		CBL(cm^2)	WT(kg^2)	COR(cm^2)	CBL(cm^2)
Year	20	19.96	434.4	3.16	2.92
Sires/year	275	0.69	7.4	0.43	0.42
Hirsel	3	8.73	683.9	0.91	0.91
Ewe age	4	38.36	902.8	0.92	0.95
Sex	1	32.52	407.2	4.61	5.81
Birth type	2	42.92	547.6	5.90	6.17
Birth date - linear	1	22.46	2438.4	15.81	0.70
- quadratic	1	1.17	0.6	0.89	0.45
Weight - linear	1	-	-	-	65.11
- quadratic	1	-	-	-	10.63
Residual	4562	0.277	5.22	0.122	0.119*

*Residual d.f. for this model was 4560

for CBL, 22.7% for WT and only 6.5% for COR. Clearly, much of the environmental variation in CBL and WT was common to both traits so that adjustment of one for the other removed a susbtantial amount of this common environmental variaion.

In addition, Table 4.4 also contains the analysis of variance of CBL when WT and $(WT)^2$ were included as covariates. A comparison of this trait with COR shows that the fixed linear adjustment used was almost as effective in reducing the residual error variance as would have been achieved by fitting the actual relationship between CBL and WT. The estimated relationship between CBL and WT is shown in Figure 4.1 indicating significant curvilinearity, but the linear component was very close to the actual linear function used for adjustment.

The effects of ewe age, sex and birth type on the measured and estimated traits are shown in Table 4.5 as least squares constants standardised by the phenotypic standard deviation of each trait. The standardised estimates for CBL and WT showed very close quantitative agreement with each other probably indicating a common basis for these environmental effects. Increasing ewe age up to 5 years resulted in increased length of cannon bone and body weight. Males were larger than females in both bone length and body weight, while lambs born as singles were larger than twins. Differences between twin born and reared lambs and others are not necessarily due to birth type effects alone as these lambs and their dams were grazed separately after birth leading to possible confounding with nutritional differences. As expected from the analyses of variance, the least squares constants for COR were much smaller than

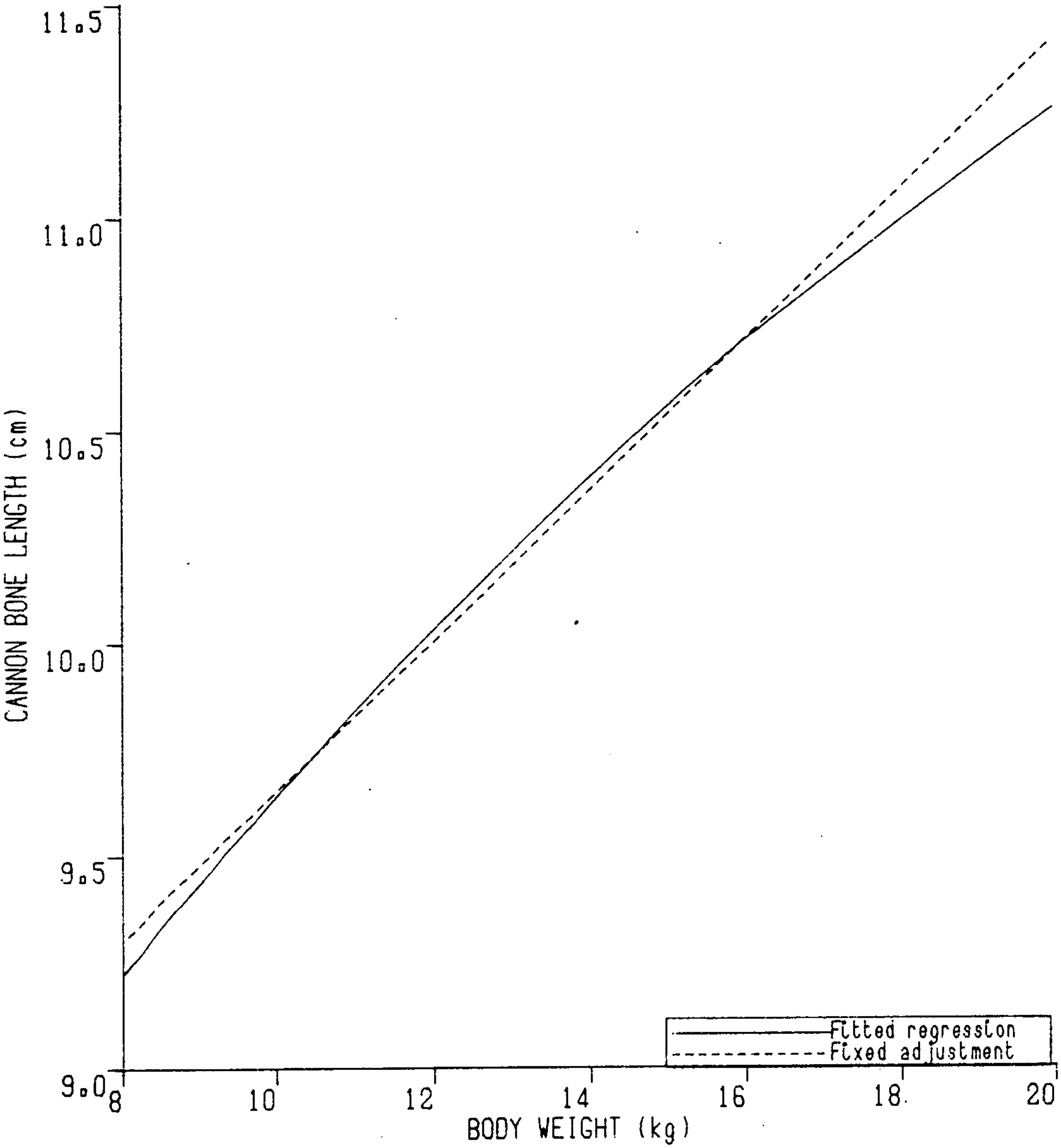

FIGURE 4.1. Regression of cannon bone length on body weight as assumed by the fixed adjustment and as estimated from the data.

Table 4.5. Least squares constants for ewe age, sex and birth/rearing type effects on CBL, WT and COR, standardised by the phenotypic standard deviations appropriate to each trait.

Effect and level	L.S. Constants/phenotypic standard deviation		
	CBL	WT	COR
Ewe age - 2 years	-.62a*	-.72	-.13a
- 3 years	-.13b	-.15b	-.03ab
- 4 years	+.15c	+.22c	-.01ab
- 5 years	+.32d	+.35d	.08b
- 6 years	+.28d	+.30cd	.09b
Sex - male	+.15a	+.13a	.08a
- female	-.15b	-.13b	-.08b
Birth/rearing type			
- single/single	+.50a	+.42a	.27a
- twin/single	-.21b	-.18b	-.10b
- twin/twin	-.29b	-.24b	-.17b
Mean	10.07cm	12.4kg	10.28cm
Phenotypic standard deviation	0.55cm	2.3kg	0.38cm

*Within each variable, deviations not followed by a common letter differ significantly ($P<0.05$)

the corresponding effects on CBL.

The influence of birth date on the traits is shown in Figure 4.2. The curved relationship for CBL indicated that the charater had probably past its linear growth phase at the time of measurement while body weight growth showed no such deviation from linearity. The combined effect of the two relationships was that the influence of birth date on CORCBL was inverted compared with that for CBL. Thus, lambs born early (that is, were older than average at the time of measurement) were over-adjusted by the fixed linear adjustment of CBL for WT.

(ii) Genetic and environmental components of variance

Estimates of heritability and standard error for each trait, using a variety of estimators, are shown in Table 4.6. There were no significant differences between the estimates for males and females for any trait by any method and so the estimates have been combined across sexes to give a pooled estimate for both the heritability and its standard error.

Estimates of the components of the phenotype variance were made assuming that dominance variances and covariances were zero (Table 4.7). The estimates of direct-maternal additive covariances were very small and imprecisely estimated. A further set of estimates were obtained by setting this direct-maternal genetic covariance to zero (Table 4.7). Some additive maternal variance in both CBL and WT was apparent. Maternal environmental variance and covariance between direct and maternal environmental effects were significant components of variance for CBL and WT, but virtually zero for COR. From the estimates contained in the lower half of

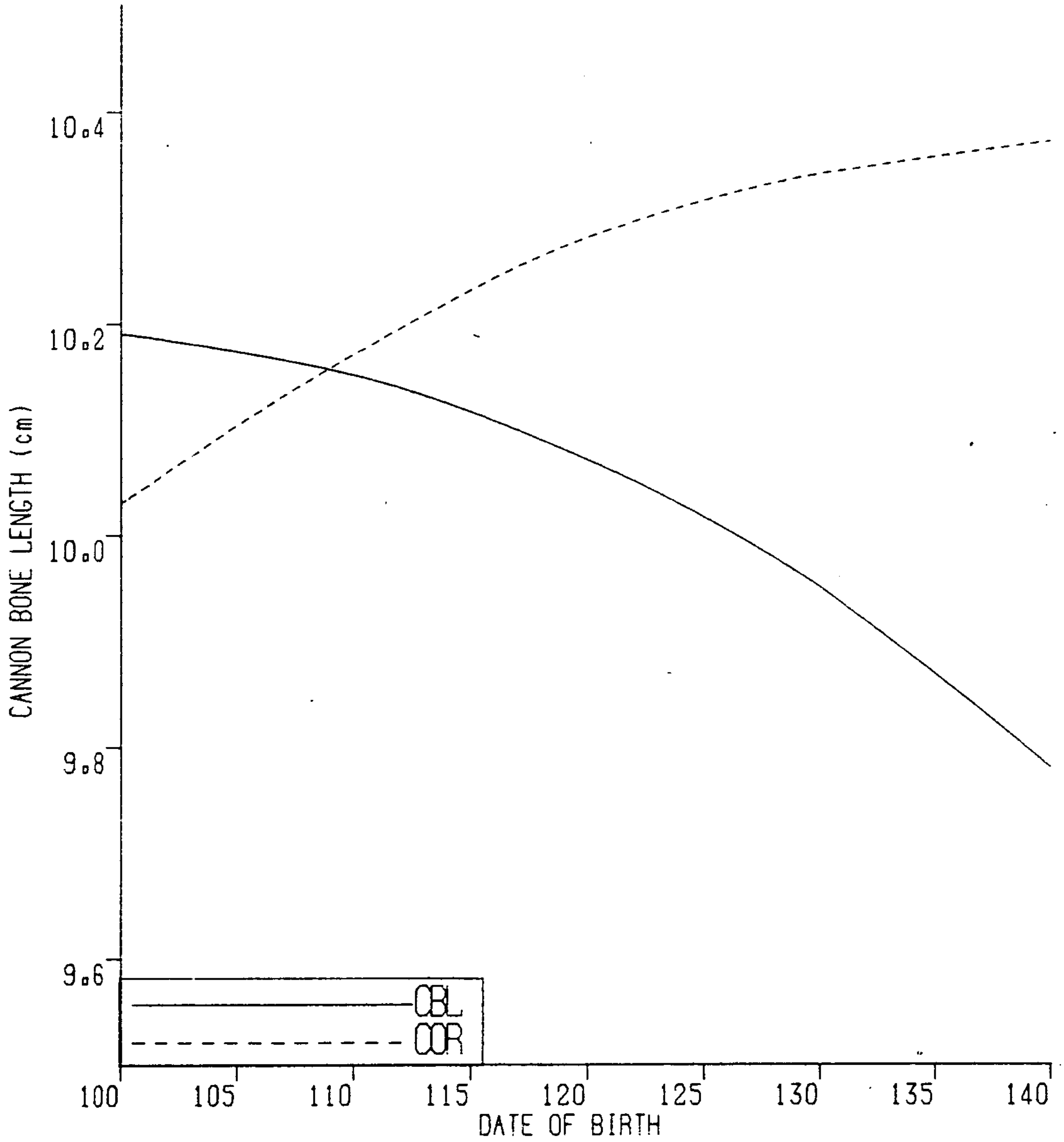

FIGURE 4.2. Regressions on birth date of cannon bone length (CBL) and adjusted cannon bone length (COR).

Table 4.6. Heritability estimates for CBL, WT and COR

Estimate type*	Heritability			Approximate standard error
	CBL	WT	CORCBL	
PHS	.33	.08	.53	±.04
O-S	.40	.14	.73	±.05
GS[O-GP]	.32	.09	.35	±.16
O-GD	.39	.16	.43	±.10
GMSQS	.14	.09	.07	±.08
O-D	.61	.37	.57	±.04
MHS	.26	.30	.16	±.02

*See Table 2 for explanation of abbreviations

Table 4.7. Estimates of the proportion of phenotypic variance accounted for by the causal components.

Trait	(CO) Variance component (±standard error)$^+$:-					
	σA^2_o	σA^2_m	σA_oA_m	σE^2_m	σE_oE_m	σE^2_o
1. Dominance variance ≡ 0						
CBL	0.36±.02	0.04±.07	0.01±.04	0.12±.05	0.09±.03	0.47
WT	0.10±.02	0.03±.07	0.02±.04	0.22±.05	0.09±.03	0.63
COR	0.60±.05	-0.07±.18	-0.03±.12	0.11±.12	0.06±.09	0.39
2. Dominance variance and σA_oA_m=0						
CBL	0.36±.02	0.05±.03		0.12±.02	0.10±.02	0.47
WT	0.10±.02	0.07±.04		0.21±.04	0.10±.02	0.62
COR	0.56±.04	**		0.02±.05	0.01±.04	0.42

$^+$ (CO) Variance component as a proportion of the phenotypic variance

* σA_o^2 = direct additive genetic variance; σA^2_m = maternal additive genetic variance; σA_oA_m = direct maternal additive genetic variance; σE^2_o = direct environmental variance; σE^2_m = maternal environmental variance; σE_oE_m = direct maternal environmental variance

** negative estimate for component set to zero and the remaining components re-estimated.

Table 4.7, the correlation between maternal and direct environmental effects were 0.42 and 0.27 for CBL and WT respectively.

(iii) Selection effects

Apart from treating all heritability estimates as independent, it has also been assumed that there has been no selection within this control flock. Any selection, whether direct or indirect, for the traits examined would be readily seen as a change in variance of the parents compared with unselected animals. The variance of sires and their unselected sons and of dams and their unselected daughters for CBL, WT and COR were obtained from analyses estimating the covariance between parents and progeny (Table 4.8). The variances of dams were slightly lower than that of their daughters for all traits. However, the sire variances were considerably smaller than those of their sons.

Directional selection in each of the traits was examined by computing cumulative selection differentials from 1954 to 1974 in the control flock. The average selection differentials applied each year in standard deviation units were 0.14, 0.16 and 0.04 for CBL, WT and COR respectively. In the case of COR, however, there was evidence of stabilising selection. The effect of these two types of selection would be to bias downwards heritability estimated by between-sire variances, paternal half-sib and grand maternal sire quarter-sib estimates. Although the level of bias in these data was estimated to be less than 10 <u>percent</u> of the estimated heritability, biases of this magnitude may be sufficient to considerably disturb the estimates of some or all of the variance

Table 4.8. Variances among parents and unselected progeny for CBL, WT and COR.

	Variances		
	CBL(cm^2)	WT(kg^2)	COR(cm^2)
Sires	0.203	4.3	0.064
Sons	0.305	5.9	0.144
Dams	0.237	4.0	0.130
Daughters	0.266	4.7	0.137

components.

(iv) Phenotypic and genetic correlations

Genetic correlation estimates obtained from paternal half-sibs, offspring-dam and maternal half-sibs, together with phenotypic correlations, amongst the three traits are presented in Table 4.9. Adjustment of CBL for its assumed relationship with WT reduced the phenotypic correlation from 0.73 to effectively zero.

The expectations of the genetic correlations are different by the three methods due to the influence of maternal effects. Paternal half-sib estimates contain only direct genetic covariances while offspring-dam estimates contain both direct and maternal genetic covariances. Maternal half sib estimates contain both maternal genetic and maternal environmental covariances with only a small contribution from direct genetic covariances. Estimates of the covariance between the three traits are shown in Table 4.10 where each contain one-quarter of the additive direct genetic covariance. These were derived from the between-sire covariance for PHS, one half of the offspring-dam covariance for O-D, and the between-dam covariance for MHS. There was little evidence of any maternal genetic covariance or environmental covariance operating betweeen COR and either CBL or WT, since the estimated covariances by the three estimation methods were almost identical. For CBL and WT, however, the covariance between the traits included not only direct additive covariance but also maternal additive covariance and some maternal environmental covariance.

Table 4.9. Phenotypic and genetic correlations between CBL, WT and COR.

Traits correlated		Genetic correlations (±s.e.) by:-			Phenotypic correlations
		PHS	O-D	MHS	
CBL	WT	.55 ± .11	.68 ± .05	.84 ± .02	.73
CBL	COR	.91 ± .03	.80 ± .03	.53 ± .05	.67
WT	COR	.18 ± .16	.10 ± .05	.00 ± .07	-.02

Table 4.10. Covariance between CBL, WT and COR estimated by PHS (containing $1/4\sigma A^2o$ in component traits), O-D ($1/4\sigma A^2o + 1/4\sigma A^2m$) and MHS ($1/4\sigma A^2o + \sigma A^2m + \sigma E^2m$).*

Traits correlated		Covariances estimated from:-		
		PHS	O-D	MHS
CBL	WT	0.029	0.075	0.319
CBL	COR	0.020	0.020	0.024
WT	COR	0.008	0.008	0.001

*σA^2_o = direct additive genetic variance

σA^2_m = maternal additive genetic variance

σE^2_m = maternal environmental variance

DISCUSSION

Statistical analysis

Before discussing the results, some comments should be made concerning the estimation procedure of the variance components. Previous attempts to use a similar approach can be found in the literature, particularly with beef cattle (Hohenboken and Brinks, 1971; Koch, 1972). There are three areas of difficulty with the approach:

(i) The heritability estimates are assumed to be independent. The component estimates made in this way will be biassed if any of the observed family covariances are correlated (Eisen, 1967). Since virtually the same data set was used for each analysis, only the classification of records changing, such correlations among the components will exist.

(ii) Any selection operating, particularly amonst potential sires, will introduce a bias into the heritability estimates.

(iii) It was assumed that dominance effects were zero. Since dominance and environmental variances and covariances were completely confounded, this assumption was only used to estimate the correlation between direct and maternal environmental effects. The extent to which this assumption is not reasonable is unknown.

The combined effect of these difficulties and the estimated sampling variance of the components was to make inferences on certain components very dubious. In particular, the genetic covariance between direct and maternal effects could only be estimated very imprecisely in the presence of an environmental covariance between direct and maternal effects. An analogous situation has arisen in beef cattle studies involving growth rate to weaning. Koch and Clark (1955) originally proposed that there was a strong, negative genetic covariance between direct and maternal effects where the environmental covariance was assumed zero. Subsequently, Hobenboken and Brinks (1971) and Koch (1972) have suggested a moderate negative environmental covariance between maternal and direct effects on growth but a relatively small component for the genetic covariance. The important point is that simultaneous estimation of both genetic and environmental covariance substantially affects both the separate estimates of these components (Hohenboken and Brinks, 1971, Koch, 1972) and the relative precision of the estimates (Table 4.7). It remains doubtful that analysis of data from random-bred lines will ever generate a satisfactory estimate of the genetic covariance between maternal and direct effects, and that such estimates would be best derived from designed selection experiments.

Genetic and environmental variances and covariances

Cannon bone length was shown to have a moderate amount of additive genetic variation available such that response to individual selection should be possible. Relatively small amounts of additive variance were available for body weight. Some additive maternal variance was apparent in both traits which would increase the expected response to selection on phenotype above that expected from paternal half sib estimates of heritability. Pattie (1965) and Hanrahan (1976) also reported maternal genetic variation in sheep for body weight at weaning, as evidenced by differences between heritability estimators. The milk production of the dam would be an obvious source of some of this maternal genetic variance (Pattie and Trimmer, 1964).

Length of cannon bone and body weight had a correlation of direct genetic effects of +0.55. This correlation was smaller than the phenotypic correlation, indicating an 'environmental' correlation of 0.81. However, this 'environmental' correlation also includes genetic covariance arising from additive maternal effects. Given the difference in covariance estimated from offspring-dam compared with paternal half sib estimates (Table 4.10), it was apparent that maternal genetic affects on bone length and body weight were highly correlated. Again, milk production of the dam would be expected to influence both bone length and body weight amongst suckling lmabs.

The most outstanding result was that of a positive correlation between maternal and direct environmental effects. No previous estimates of such a correlation have been reported in sheep. The explanation of this effect probably lies in the unique behaviour of hill sheep in the United Kingdom. Ewes were 'hefted' on to the farm in four separate hirsels, or areas of the hills. In addition, hefting results in small groups of ewes selecting relatively confined territories for grazing within a hirsel, and a ewe will tend to remain in this territory for her entire productive lifetime. Similarly, after lambing, a ewe will return to her specific area with her lambs, and the daughters will subsequently remain near their mother's territory for their lifetime. Therefore, specific environmental effects (such as grazing conditions, shelter) operating on a ewe are likely to be closely related to the environmental effects operating on her progeny early in life because of the similarity in physical area under which both the ewe and her progeny are raised. This would manifest itself as a covariance between maternal (ewe) and direct (progeny) environmental effects. The size of the correlation is such that offspring-dam estimates of heritability for any trait in hill sheep with a maternal environmental effect are likely to be substantially over-estimates of the rate of response to selection.

Cannon bone length adjusted for body weight

The fixed adjustment procedure used to correct cannon bone length for body weight differences had a number of effects:

(i) Identifiable environmental sources of variation such as ewe age and birth/rearing type were largely removed by the adjustment. Thus, selection could operate on estimated values without the need to allow corrections for these sources of variation, with little loss of accuracy.

(ii) Random environmental variance was substantially reduced.

(iii) Maternal additive genetic variance was effectively removed.

(iv) A substantial amount of the genetic covariance between cannon bone length and body weight was removed leading to a reduction in the genetic correlation with weight.

The success of the adjustment procedure was primarily due to the high correlations between maternal genetic effects and between environmental effects affecting both traits. Adjustment of one trait for deviations in the other effectively removed most of this common variance. The net effect was to increase the heritability of the character, since there was a small reduction in additive genetic variance but a proportionally greater reduction in environmental variance. The genetic correlation between the adjusted character and cannon bone length was still effectively unity while the genetic correlation between cannon bone length and body weight was reduced from 0.55 to 0.18 after adjustment. Expected correlated response in cannon bone length to selection on the adjusted trait was similar to the expected response to selection on phenotype for cannon bone length. However, all the response on the adjusted trait would derive from direct additive genetic improvement, 10 percent more than the equivalent direct genetic response from selection on cannon bone length. In addition, expected correlated response in body weight would be smaller when selection was based on adjusted rather than unadjusted cannon bone length.

CONCLUSIONS

Cannon bone length (CBL) and body weight (WT) measured at eight weeks of age were shown to be complex traits involving genetic and environmental components of variance from both direct (lamb) effects and maternal (dam) effects. The proportion of the phenotypic variance that was geneticlly derived was 41 percent for CBL (36 percent direct and 5 percent maternal) and 17 percent for WT (10 percent direct and 7 percent maternal). Of the remaining environmental variance in both traits, about two-thirds arose from direct environmental effects while one-third arose from maternal environmental effects and the covariance between diretc and maternal environmental effects. Most of the maternal genetic and maternal environmental variance in CBL and WT were from a common source since adjusting CBL for its phenotypic regression on WT (derived trait, COR) resulted in a simple trait in which only direct genetic and environmental effects were important in influencing phenotype.

CHAPTER 5

SELECTION FOR AN INDEX OF CANNON BONE LENGTH WITH RESTRICTION ON BODY WEIGHT:

RESPONSES IN THE INDEX AND ITS COMPONENT TRAITS

INTRODUCTION

In Chapter 4, rates of response to selection for an index of length of cannon bone with restriction on body weight at eight weeks of age in Scottish Blackface sheep were predicted from parameter estimates in a base population and an 'unselected' control flock. In this Chapter the actual rates of response in lines selected for and against the index are examined. The realised direct responses in the index and its component traits are reported, and evidence for changes in phenotypic and genetic parameters with selection is assessed.

MATERIALS AND METHODS

Description of lines

The location, environment, sheep and their management have been described in Chapter 3.

Cannon bone length (CBL) and body weight (WT) were measured on all lambs at about eight weeks of age and the index (COR) was calculated for each animal as:

$$\underset{(\text{cm})}{\text{COR}} = \underset{(\text{cm})}{\text{CBL}} + 0.176\,(13.6 - \underset{(\text{kg})}{\text{WT}})$$

This index was then the primary selection criterion used.

The formation of the selection lines and the methods of selection used were detailed in Chapter 3.

The three flocks considered here are the unselected control line (CONTROL) in which selection was at random, a line selected for high COR (LONG) and a line selected for low COR (SHORT) at eight weeks of age.

Selection differentials

A previous analysis of environmental effects on COR (Chapter 4) had shown that hirsel, ewe age, birth type and birth date accounted for only small amounts of variation. Selection differentials and responses were estimated for the selection criterion using adjustments for these effects estimated from the CONTROL line (Chapter 4). The differences between years and sexes in mean COR and its variance were rather small, so that no adjustment for either mean or standard deviation in the CONTROL line was used. Cumulative individual and total selection differentials for all animals in the LONG and SHORT lines were calculated as previously described (Chapter 3).

The individual selection differentials represent phenotypic deviations on which mass selection would be expected to operate. However, the parentage of each ram was also considered before sires were chosen. Such considerations of parentage led Purser (1980) to assume that the selection was more appropriately within-sire family rather than mass selection. A retrospective analysis of the relative index weights applied to between- and within-sire family deviations was attempted to test this assumption. Sire family means were estimated and differences estimated between these means and the overall flock mean in each year to obtain between sire family deviations. Within-sire family deviations were then calculated as the difference between an individual's COR and the appropriate sire family mean. Since almost all directional selection on COR was restricted to males, the retrospective analysis of the method of selection was undertaken in males only. All rams born between 1956 and 1973 (since no 1974 born rams were selected as replacements) in the LONG and SHORT flocks were classified as chosen as sires or not. This binomial trait was examined with a logit transformation using the iterative generalised linear models program, GLIM (Baker and Nelder, 1978) in order to see how precisely the actual selection method could be specified. The reductions in deviance obtained by fitting either the individual's phenotypic deviation or its within-sire family deviation were estimated and further models were fitted to see if including the between-family deviation resulted in any further reduction in deviance. The goodness-of-fit of a final model was tested by a procedure suggested by Tsiatis (1980). Animals were classified into 9 equally sized classes (since about 11 per cent of all males were selected) according to their fitted values, and for further reductions in deviance were estimated using this coarse classification The analyses were done separately for each selection line initially. However, there were no significant differences between lines and so the results from analyses including all males from both selection lines are presented.

Realised heritability

Realised heritability was estimated as the regression of cumulative response on cumulative selection differential. Initially, symmetry of response was examined by estimating this regression for the LONG line as a deviation from the CONTROL and similarly for the SHORT line. In this case, cumulative response to selection was calculated as the difference between the mean COR in each selection line and the mean COR in the CONTROL line in each year. Where differences between the regressions from each selection line were not apparent, the CONTROL was ignored and a regression based on the divergence between LONG and SHORT lines in each year for both cumulative selection differentials and response.

As pointed out by Hill (1972a), the standard error of an unweighted regressions of response on selection differential is not an appropriate estimate of the standard error of the realised heritability. The regression variance is biassed downwards since the individual year observations are treated as independent whereas they are correlated with each other due to genetic drift. Hill (1972a) developed an approximate variance of a realised heritability estimate appropriate to an unreplicated selection experiment with observations at discrete generations. Johnson (1977) showed that the asymptotic rate of drift accumulation was an underestimate of the actual rate of drift in the early years of a selection line with overlapping generations. Using the approach of Johnson (1977) and Hill (1971), the expected variance-covariance structure of direct responses to selection in each year of this experiment was derived. A generalised least-squares solution for the realised heritability was possible, with an appropriate variance, from:-

$$b = (X'V^{-1}X)^{-1} X'V^{-1}Y$$

where b = regression coefficient of cumulativeresponse on cumulative selection differential

X = vector of cumulative selection differentials

Y = vector of cumulative direct response

V = variance-covariance matrix of cumulative responses

In an appendix to this chapter the methods used are described in detail. In addition, the estimates of realised heritability and its standard error by unweighted regression and by generalised least squares are compared.

The estimated regressions were all forced through the origin since all lines were derived from the same base population. The significance of a quadratic regression coefficient was also tested.

Realised correlated responses in the components of the index

Correlated responses in CBL and WT in both selection lines were examined. Individual records were first adjusted for the effects of hirsel, ewe age, birth type and birth date as estimated from an analysis of the CONTROL line (Chapter 4). These fixed effects were also estimated within the selected lines and similar estimates obtained for all sources of variation other than ewe age, indicating no line x environmental effect interaction. The ewe age effects in the selected lines were biassed by the responses to selection and, for this reason, adjustments for the CONTROL line data were used across all lines. Cumulative correlated responses to selection were calculated as the difference between the mean CBL and WT in each selection line and the mean CBL and WT respectively in the CONTROL line in each year of the experiment. Realised correlated regressions were estimated as the regression (through the origin) of cumulative correlated response on the flock cumulative selection differential for COR. Where differences between the regressions from each selection line were not apparent, the CONTROL was ignored and the regression re-estimated from divergence between the LONG and SHORT lines in each year for both cumulative selection differentials and correlated responses.

An appropriate variance-covariance matrix for the correlated responses was derived in a similar manner to that for the direct responses. Again, the formulation is described in the Appendix to this Chapter. This variance-covariance matrix was used to derive a generalised least-squares solution for the realised correlated regression coefficients and their standard errors.

Phenotypic and genetic parameters in the selected lines

Estimates of heritability of COR, COR and WT, and the phenotypic and genetic correlations between these traits were made within both the LONG and SHORT selected lines. The analyses were performed on the records after first adjusting the traits for the environmental effects of hirsel, ewe age, birth type and birth data as estimated from the CONTROL flock data (Chapter 4). Genetic parameters were estimated by paternal half-sib analyses of variance and offspring-dam regressions as described in Chapter 3. The analyses were done separately for males and females and the estimates pooled.

RESULTS

Methods of selection

The likelihood of a ram being selected as a sire was examined by successively fitting effects to a linear model and testing for the significance of reductions in deviance. Year of birth, flock and their interaction had no significant effect since almost equal numbers of sires were selected in each flock in each year from similar numbers of available males. The phenotypic deviation of an animal's COR from the mean of that year resulted in a large, significant reduction in deviance although adding between sire family deviation resulted in a further reduction in deviance (Table 5.1) showing that the selection applied on the trait was not simply mass selection. Alternatively, adding between sire family deviation to a model already containing the within sire family deviation resulted in a significant reduction in deviance (Table 5.1) so that the selection applied was not equivalent to within sire family selection as assumed by Purser (1980). Comparison of the two models in Table 5.1 in the effect of adding between sire family information would, in fact, suggest that the selection was nearer mass selection than within sire family selection. From the second model, the fitted index of selection was:-

$$I = WF + 0.72\ BF$$

where WF = within-sire family deviation

BF = between-sire family deviation

Of course, the appropriate coefficients of the between sire family

Table 5.1. Analysis of deviance for the probability of selection amongst rams.

Model	d.f.	Residual deviance	Variable	d.f.	Marginal deviance (χ^2)
Mean (μ)	3421	2353			
μ + Year(Y)	3404	2347	Y	17	6
μ + Y + Line (L)	3403	2346	L	1	1
μ + Y + L + phenotypic deviation (PD)	3402	1323	PD	1	1023*
μ + Y + L + PD + between family deviation (BF)	3401	1310	BF	1	13*
μ + Y + L + within family deviation (WF)	3402	1407	WF	1	939*
μ + Y + L + WF + BF	3401	1310	BF	1	97*
μ + Y + L + WF + BF + class (C)$^+$	3393	1248	C	8	62*
u + Y + L + C	3395	1279	C	8	1067*

* X^2 significant ($P<0.05$)

$^+$ Class. This variable was derived from the individual fitted values for the model (μ + Y + L + WF + BF). Rams were separated into one of nine (9) equally sized classes according to their ranked fitted values in order to test for goodness-of-fit. See text.

deviation for mass selection and within sire family selection would be unity and zero respectively.

This retrospective index was not perfect in describing the selection process. From the goodness-of-fit model (Table 5.1) the index accounted for about 95 per cent of the total reduction in deviance one would expect with a complete description. This is illustrated by the proportion of rams actually selected in each of the nine fitted classes (Table 5.2). If the index of selection was appropriate, there would be 97 per cent of selected rams in class 9 and zero in all other classes. There are a number of possible reasons for this lack of agreement:-

* mortality of rams between measurement (at 2 months of age) and use as sires (7 months)
* selection on other traits such as those employed in the visual culling

Including phenotypic deviation for WT into the index of selection, however, only marginally improved the goodness-of-fit.

* variation in family size
* the restrospective index is linear whereas the reasons previously given for accounting for parentage would suggest independent culling levels, a process not adequately described by a linear model
* simple errors of selection

There are clearly many inherent problems in attempting to statistically impose a single retrospective index of selection on data such as these. However, the results do demonstrate that

Table 5.2. Proportion of rams selected from each of nine equal classes partitioned according to increasing value of the fitted index, I = WF + 0.72 BF.

Class	Proportion of rams selected as sires
1	0
2	0
3	0
4	0.003
5	0.011
6	0.021
7	0.070
8	0.277
9	0.597

simplistic assumptions of simple mass selection or within sire family selection operating were not appropriate.

Direct response to selection

Cumulative selection differentials applied in the LONG and SHORT lines are shown in Figure 5.1. These were calculated for phenotypic deviations and so are relevant to mass selection. The implications of the actual method of selection will be considered later. Consistent selection for COR was applied in both the LONG and SHORT lines while the response to selection was also consistent in both directions (Figure 5.2) with no evidence of any asymmetry of response or sex differences. Thus, only divergence between the LONG and SHORT flocks has been considered (Figure 5.2). The weighted linear regression of response on selection differential was 0.489±0.022 (see Appendix). Fitting a quadratic term for selection differential resulted in a predicted regression (with standard errors) of (Figure 5.2):-

$$R = \underset{(\pm.048)}{0.530}\ S - \underset{(\pm.008)}{0.009}\ S^2$$

where R = cumulative divergence (cm)

S = cumulative selection differential (cm)

These regression estimates were not appropriate estimates of the realised heritability since the method of selection was not simple mass selection. We will first derive the expected response

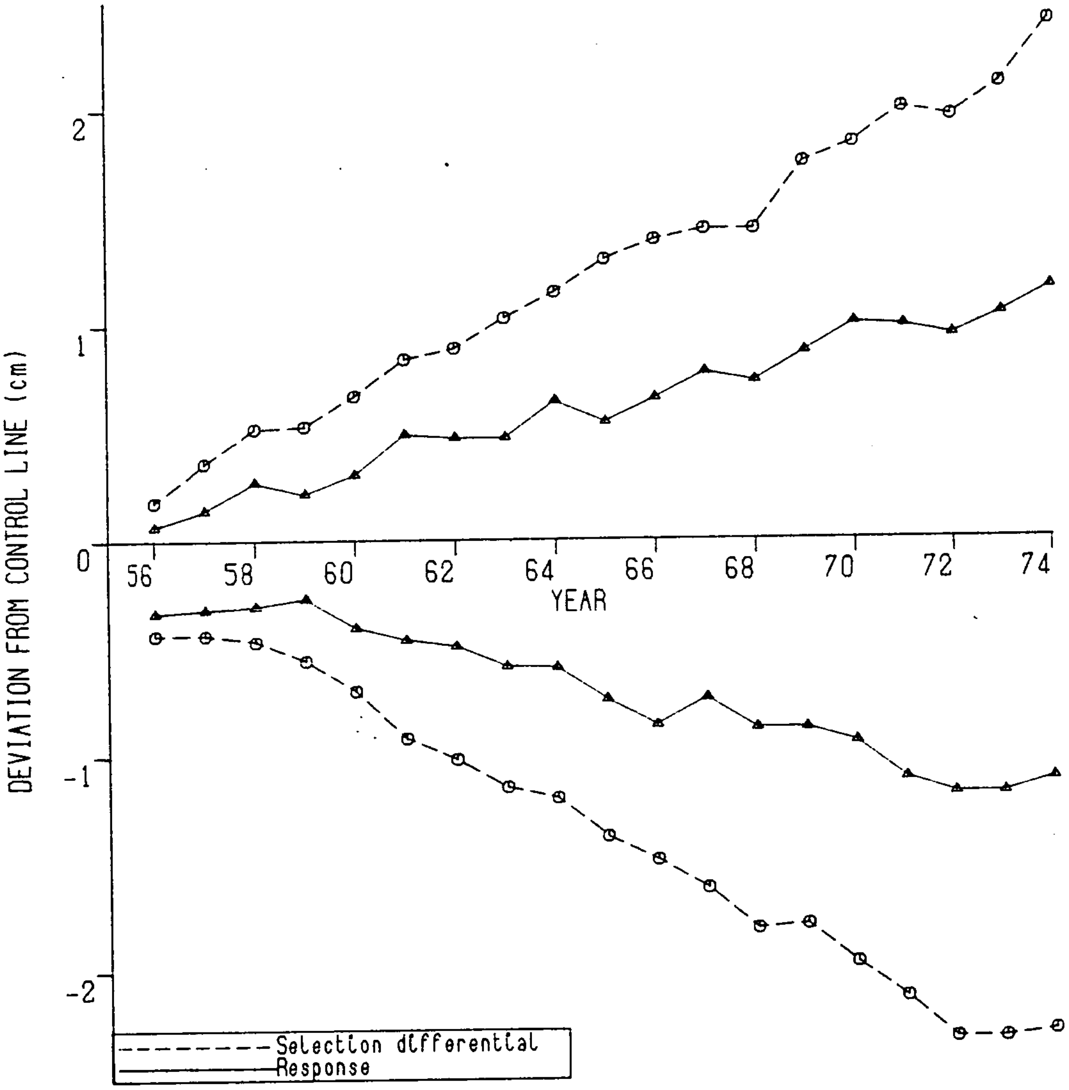

FIGURE 5.1. Cummulative selection differentials and cummulative responses for COR in the LONG and SHORT lines.

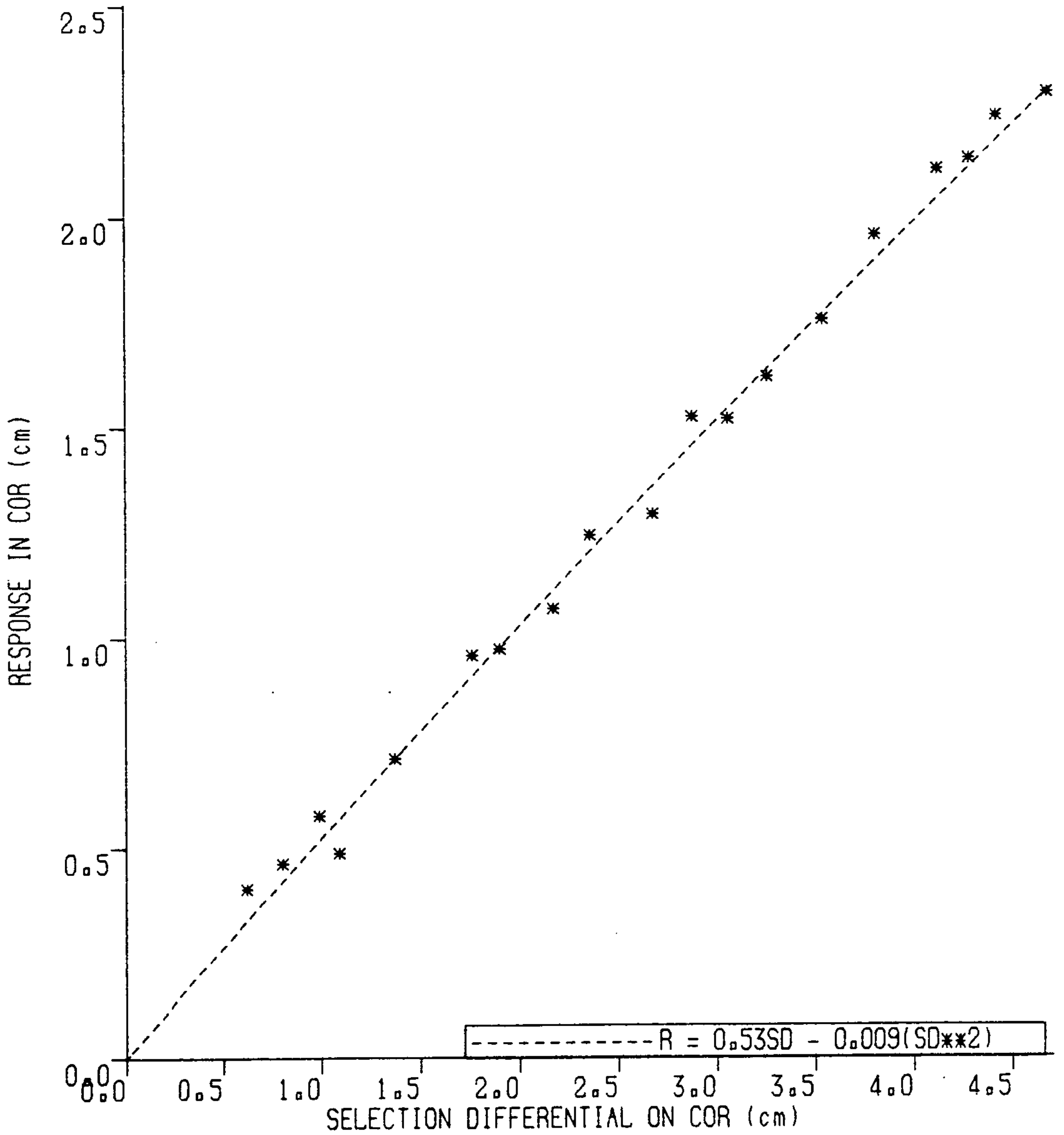

FIGURE 5.2. Regression of cummulative response on cummulative selection differential for the divergence between LONG and SHORT lines.

to selection on the retrospective index of selection, I = WF + 0.72 BF. Since the within- and between-family deviations are uncorrelated, the expected phenotypic and additive genetic variances of the index could be expressed as follows (from Falconer, 1981):-

$$V_P(I) = V_P(WF) + (0.72)^2\, V_P(BF)$$

$$= \frac{(n-1)(1-t)\sigma_P^2}{n} + (0.72)^2 \frac{\{1+(n-1)t\}\sigma_P^2}{n}$$

$$V_A(I) = \frac{(n-1)(1-r)\sigma_A^2}{n} + (0.72)^2 \frac{\{1+(n-1)r\}\sigma_A^2}{n}$$

where n = family size

r = coefficient of relationship between family members

t = intra-class correlation between family members

σ_P^2 = phenotypic variance

σ_A^2 = additive genetic variance

The regression of response on selection differential would have an expected value equal to the realised heritability of the actual index of selection (or $V_A(I)/V_P(I)$). By substituting $h^2 = \sigma_A^2/\ \sigma_P^2$ and collecting terms, the expected value of the realised regression (b) was:-

$$b = h^2 \frac{\{n-0.48(1+r(n-1))\}}{\{n-0.48(1+t(n-1))\}}$$

In this experiment the weighted average sire family size was 18.8. Ideally, with one offspring per dam, then r = 0.25 for members of a sire family and $t = rh^2$ since sires were allocated to dams at random so that there was no environmental variance shared by members of a sire family. Actually only 10 per cent of progeny in the experiment were pairs of full-sibs, and adjusting r and t for the true relationship between family members had a trivial effect on the expectation of the regression and so it has been ignored. For b = 0.49, solving equation [1] for h^2 gave an estimated realised heritability of 0.52.

At the conclusion of the experiment, the cumulative direct response to selection estimated as the predicted divergence between the LONG and SHORT lines was 2.29 cm. This divergence represented a total response of almost 6 phenotypic standard deviations or 22 _per cent_ of the CONTROL line mean.

Correlated responses in index components

There was no evidence of any differences between sexes in the regressions of correlated response for CBL and WT on cumulative selection differential for COR. Based on the estimated difference in variance between sexes in the CONTROL line, correlated responses amongst males for CBL and WT might be expected to be 3 and 10 _per cent_ higher (respectively) than amongst females, which are small effects in relation to the standard errors of the regressions. Responses have been pooled across sexes without adjustment and the correlated regressions are presented in Table 5.3 for CBL and WT in both the LONG and SHORT selected lines separately. The method of estimation of these regressions has been described in the Appendix.

There was some evidence of asymmetry of response with greater correlated regressions for both CBL and WT in the SHORT line (Table 5.3), although the regression coefficients were not significantly different from each other. However, this observed asymmetry, although small, may be biologically real. As already

Table 5.3. Realised correlated responses, expressed as regressions (± standard error) of response in CBL (cm) and WT (kg) on selection differentials for COR (cm).

	CBL	WT
Deviations from CONTROL		
LONG - CONTROL	0.46±.05	-0.05±.13
SHORT - CONTROL	0.55±.05	0.25±.12
Divergence		
LONG-SHORT	0.517±.024	0.14±.06

stated, one of the major traits on which animals were visually culled in all lines was body weight. Cumulative selection differentials for WT were calculated for all flocks (Figure 5.3). The phenotypic correlation between WT and the primary selection criterion, COR, was effectively zero so that the selection differentials applied for WT can be considered independently of the selection applied for COR. From Figure 5.3, the total selection applied for WT was somewhat lower in the LONG line than in the other two lines, which might have been expected when the culling criterion was a visual assessment of body size. Accounting for the expected responses from this secondary selection reduced the apparent asymmetry of the correlated responses in the index components. However, separating expected responses arising from 'primary' and 'secondary' selection is an argument for considering the lines to be selected for a multiple trait objective. A more appropriate description of responses under multi-trait selection is considered subsequently.

Realised regressions of cumulative divergence in the correlated traits on cumulative selection differential for COR are presented in Table 5.3. As measured at the end of the experiment, the total correlated response in CBL of 2.42cm was slightly larger than the total direct response in COR of 2.29cm. When divergence was estimated in phenotypic standard deviation units, the correlated response in CBL was 4.5 compared with 5.9 units of direct response. The total correlated response in WT at the end of the experiment was only 0.6kg or 0.3 phenotypic standard deviations.

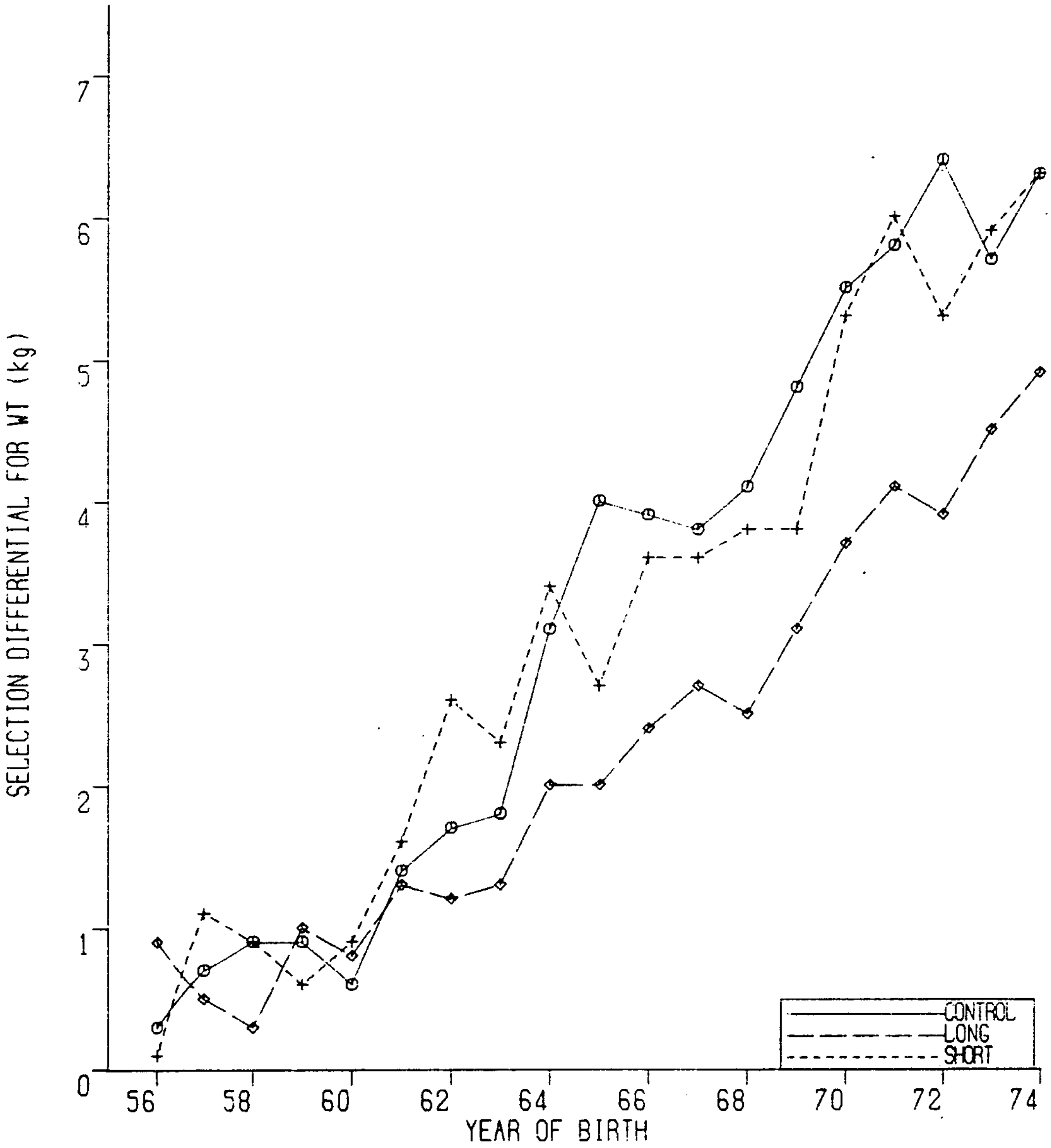

FIGURE 5.3. Cummulative selection differentials for body weight in the LONG, CONTROL and SHORT lines.

Responses from two-trait selection

If it is assumed that the selection lines were selected on an index of COR and WT, the realised genetic variances for the two traits and the covariance between them could be estimated as described in the Appendix. The estimated parameters are shown in Table 5.4 and compared with the estimates obtained from an analysis of the direct responses in COR and the correlated responses in WT. The two-trait model yielded an estimate of the realised genetic variance in WT which was previously assumed from base population parameter estimates. The estimate was equivalent to a realised heritability of 0.13±0.11 compared with the base population estimate of 0.10±.02. The standard error of the realised heritability was high because the experiment was not designed to estimate this parameter (see Appendix). The realised estimates for genetic variance in COR and genetic covariance were virtually identical in both size and standard error to those obtained from the single-trait model. This correspondence was largely fortuitous because the phenotypic and genetic correlations between the two traits was low. Therefore it was possible to regard the lines as effectively being single character selection lines for COR since ignoring independent selection on WT resulted in little loss in efficiency of estimation and introduced minimal bias.

Selection effects on parameters

Selection resulted in small reductions in the phenotypic variance of COR and the variances of the two component traits within the selected lines (Table 5.5). The phenotypic correlations

Table 5.4. Realised estimates (± standard error) of the genetic variances for COR and WT and the genetic covariance between them from two-trait and single-trait models of selection (see Appendix for derivation).

Genetic (CO) Variance in:-	Two-trait model	Single-trait model
COR (cm^2)	0.0735±0.0033	0.0734±0.0033
COR-WT (cm kg)	0.021 ±0.013	0.021 ±0.010
WT (kg^2)	0.70 ±0.59	

Table 5.5. Phenotypic variances of COR, CBL and WT, and phenotypic correlations (± standard errors) between these traits estimated in the CONTROL, LONG and SHORT flocks.

	CONTROL	LONG	SHORT
Phenotypic variance			
COR (cm^2)	0.150	0.137	0.134
CBL (cm^2)	0.295	0.274	0.253
WT (kg^2)	5.22	5.05	4.79
Phenotypic correlation			
COR - CBL	0.65	0.63	0.61
COR - WT	-0.02	-0.04	-0.08
CBL - WT	0.72	0.73	0.71

between COR and its components were apparently unaltered except that the correlation between COR and WT was slightly more negative in the SHORT line. The fitted relationships between CBL and WT in each line were not different from each other, indicating the robustness of the phenotypic regression used for adjustment throughout the experiment.

Possible selection effects on genetic parameters (Table 5.6) were more difficult to assess due to biasses in the method of estimation. Selection itself, either directly on the trait or indirectly through a genetic correlation with another trait under selection, will reduce the apparent variance between sires leading to a downward bias in a heritability estimate from paternal half-sib analysis of variance (Robertson, 1977a). The heritability estimates for COR and CBL by paternal half-sib analyses were certainly lower in the LONG and SHORT lines than in the CONTROL line. However, between the selected lines the heritability of the two traits in the SHORT line was smaller than the corresponding estimates in the LONG line, significantly so for COR. Offspring-dam estimates of heritability in selected lines will be unbiassed for the trait under selection but biassed downwards (in most situations) for correlated traits. In these data, though, offspring-dam regressions were inflated by the presence of maternal-direct environmental covariance, particularly for CBL and WT (Chapter 4). For the character under selection (COR), the offspring-dam estimates provided no evidence of reduction in genetic variance in either selected line, while the heritabilities of the index component traits were smaller in the selected lines.

Genetic correlations estimated from selected lines present

Table 5.6. Heritabilities (± standard errors) of COR, CBL and WT and genetic correlations (± standard errors) between these traits. Estimates made by both paternal half-sib analysis of variance and offspring-dam regression within the CONTROL, LONG and SHORT lines.

	CONTROL	LONG	SHORT
Heritabilities			
(i) Paternal half-sib			
COR	0.52±0.05	0.37±.05	0.19±.05
CBL	0.33±.05	0.22±.05	0.09±.06
WT	0.08±.04	0.01±.03	0.06±.06
(ii) Offspring-dam			
COR	0.57±.04	0.57±.04	0.58±.04
CBL	0.61±.04	0.48±.04	0.50±.04
WT	0.37±.04	0.21±.04	0.21±.04
Genetic correlations			
(i) Paternal half-sib			
COR - CBL	0.91±.03	0.93±.06	0.68±.14
COR - WT	0.18±.18	0.27±.61	-0.51±.27
CBL - WT	0.55±.12	0.60±.54	0.24±.28
(ii) Offspring-dam			
COR - CBL	0.80±.02	0.86±.02	0.84±.03
COR - WT	0.10±.06	0.09±.06	0.10±.06
CBL - WT	0.68±.03	0.58±.03	0.62±.04

similar difficulties of interpretation as the heritability estimates (Table 5.6). The half-sib correlation estimates would be biassed by the selection although to a lesser degree than the heritabilities. The standard errors of genetic correlations involving WT were very large such that the moderate negative estimate between COR and WT in the SHORT line was not significantly different from the low positive estimates in the LONG and CONTROL lines. Again, the offspring-dam estimates had substantially lower standard errors but contained more than additive genetic covariance. These estimates from the different lines were very similar to each other (Table 5.6).

There have clearly been no pronounced changes in phenotypic and genetic parameters in the selected lines during the course of the experiment. However, such changes were extremely difficult to estimate with any precision using conventional analytical methods.

DISCUSSION

The regression of response on selection differential for cannon bone length adjusted for body weight was 0.489±0.004 (see Appendix). Purser (1980) reported a regression from the same data set of 0.424±0.004. This discrepancy was due to the incorrect method of accumulating selection differentials used by Purser (1980) following Turner and Young (1969) as described in Chapter 3. Accounting for the retrospective weighting of between- and within-family selection differentials and the expected variances of the observed responses, resulted in a realised heritability of 0.52 ± 0.02 over a period of about eight generations of selection. From

Chapter 4, the estimated heritability of this character in an unselected population was 0.56 ± 0.04 which was higher, but not significantly so, than the realised estimate. Bulmer (1976) has shown that selection reduces additive genetic variance, and, therefore, realised heritability due to the generation of linkage disequilibrium. With an infinitessimal model of gene effects, the expected reduction in additive genetic variance of the character under selection due to linkage disequilibrium was shown to be (Bulmer, 1980):-

$$V_{A(t+1)} = [1-h^2_{(t)}\{i(i-x)\}]V_{A(t)}/2 + V_A/2$$

where $V_{A(t+1)}$ = additive genetic variance at time (t + 1)

$V_{A(t)}$ = additive genetic variance at time (t)

V_A = additive genetic variance in base population (time t=0)

$h^2(t)$ = heritability at time (t)

i = standardised selection differential for a selected proportion of population, p

x = abscissa of the unit normal curve corresponding to p.

This expression was expanded to allow for different selection intensities in males and females, and then used to estimate the expected reduction in genetic variance at successive cycles of selection. For a realised heritability of 0.52 and the average selection intensities applied in this experiment, the expected base population heritability would be 0.57, which was very similar to that estimated in Chapter 4. From the observed responses there was some evidence of a decline in the realised heritability with time, as evidenced by the quadratic term in the regression of response on selection differential (Figure 5.2). After allowing for the actual method of selection (as described previously) the observed heritability in the base population from Figure 5.2 would be 0.56. Thus, the observed responses closely reflected expected responses both in terms of overall response to selection and the decline in response from linkage disequilibrium. The apparent effect of linkage disequilibrium was also reflected in a reduction in the phenotypic variance of the selected trait. From Bulmer (1980), a reduction of 10 per cent in phenotypic variance would be expected from the applied selection, while the observed reductions were 9 and 11 per cent in the LONG and SHORT lines respectively. Similarly, the phenotypic variances of the component traits were also slightly reduced in the selected lines (Table 5.5).

In order to compare the realised correlated responses in the components of the selection criterion with expectation, we must obtain some estimate of the realised genetic correlation. The regression of correlated response on selection differential has the following expectation:-

$b_c = r_G h_1 h_2 \sigma_2 / \sigma_1$

where r_G = genetic correlation

h_1^2 = realised heritability of selected trait

h_2^2 = realised heritability of correlated trait

σ_1 = phenotypic standard deviation of selected trait

σ_2 = phenotypic standard deviation of correlated trait

The realised heritability of the selected trait is simply the regression of response on applied selection differential (0.49 in this case). Of the remaining parameters, the realised genetic correlation and the realised heritability of the correlated trait are unknown. Estimates of the heritability of the correlated traits in the base population have been presented in Chapter 4, but we would expect the realised heritabilities to be lower than these estimates due to the observed combination of within- and between-family information in selection and the generation of linkage disequilibrium. Estimates of the realised genetic correlations were made using the base population heritability for the correlated trait and an adjusted heritability based on expected reductions due to method of selection and linkage disequilibrium (Table 5.7). The measure of agreement between the realised and predicted genetic correlations between the index and its components was very close.

CONCLUSIONS

The responses to selection in the index and its components were in very good agreement with predictions. This agreement was a reflection of the high precision of both the estimated genetic parameters in the unselected lines and the realised responses in the selected lines. The base population predictions were obtained from a very large data set with a favourable family structure for estimating parameters. The selected lines produced precise estimates of response because the experiment continued for a moderate length of time (about eight generations), had a large

Table 5.7. Realised genetic correlations between the selection index (COR) and its component traits (CBL and WT).

Trait	Realised genetic correlation			Base population estimate (± standard error)
	Method 1*	Method 2*	Approx. s.e.	
CBL	0.88	0.95	±.06	0.91±.03
WT	0.10	0.11	±.06	0.18±.16

*Method 1 - base population heritability estimates where $h^2_{CBL} = 0.36$ $h^2_{WT} = 0.10$

+Method 2 - base population heritabilities adjusted for expected effects of linkage disequilibrium and method of selection, where $h^2_{CBL} = 0.31$ $h^2_{WT} = 0.09$

effective population size in each line of about 100 animals and selection was based on a trait with a high heritability and low coefficient of variation. In addition, the assumptions that are made in predicting responses to selection from parameter estimates all proved to be valid. For example:-

- The distribution of phenotypes in the selected lines remained normal.

- The simple additive model of genetic and environmental effects was adequate with no evidence of genotype x environment interactions. In fact, there was little variation between years in the average performance of the CONTROL line with respect to the selection criterion.

- There was no evidence of large changes in the phenotypic and genetic parameters with selection.

- There was no evidence of any substantial asymmetry of response.

APPENDIX - Estimation of Responses to Selection

The regression of cumulative response on cumulative selection differential at each generation has commonly been used as the method of estimating responses to selection (Falconer 1981, Richardson et al., 1968). Over a wide range of parameter values and population structures, Hill (1972a,b) found such estimates were largely unbiassed and quite efficient. However, the variance of such simple regression estimates are inappropriate, since it is assumed that the observations on the dependent variable (cumulative response) are independent and have equal variances. With a continuing selection line, the parents of the next generation are sampled from a finite population of individuals from the current generation. This genetic sampling leads to an increasing variance of the line mean at each successive generation, and induces a covariance between the line means at different generations. To ignore these correlations and variance changes will lead to the variance about a fitted regression to be substantially underestimated.

Variance-covariance matrix of observed responses

The variance of a group mean was described by Hill (1971) firstly in a single generation and then for several generations of sampling. These variances were conditional on the observed selection differentials. The observed cumulative selection differentials at each generation of a selection experiment are usually expressed as the difference between a group mean for a selected line and a contemporary group mean for either a control line (selection in one direction) or another selected line (divergent selection). Assuming the two lines used to measure response are divergent select on lines having the same structure and similar proportional sampling of parents, the variance of observed response and would be twice that of the variance of a single line mean.

In a simplified model of selection, we assume that in each of the two lines there are M individuals recorded and N selected in each generation as the only parents of the next generation (i.e. the generations are discrete). The trait under selection has a phenotypic variance σ^2 and a genetic variance $h^2\sigma^2$ (where h^2 = heritability). Restating Hill (1971, 1972), the variance of the measure of response will contain:-

* <u>drift variance</u>. This variance accumulates over generations and in each generation comprises two parts; firstly $2\sigma^2h^2(1-h^2)/N$ for the deviation of the genetic mean of the N selected individuals about the genetic regression and, secondly, $2\sigma^2h^4/M$ for the deviation of the observed selection differentials of all recorded individuals from their true value. The second term arises because the group mean of each line varies about its true population value since only M individuals (rather than an infinite number) are recorded and so disturbs the prediction of breeding value at subsequent generations. If the two lines were initially derived from a single base population, the deviations of the selection differentials between lines will cancel each other in the first generation. In a situation of no selection (not to be confused with random selection), the sum of these two parts would be σ^2h^2/N

per generation in each line (where N=M), which is the usual expression for random drift without selection.

* error (measurement) variance. This term estimates the sampling variance of the difference between the line means about the true (or population) difference. This variance depends on the distribution of family sizes (Hill, 1971) and a number of different expressions appear in the literature, for example:-

$2\sigma^2(1-0.5\ h^2)/M$ for families of equal size
$2\sigma^2(1-0.5\ h^4)/M$ if family size is Poisson distributed
$2\sigma^2/M$ an approximation

In a selection experiment where selection differentials were computed for each individual, the between family information is effectively weighted by the number of individuals per family so that it approaches an equal family size situation. So, $2\sigma^2(1-0.5\ h^2)/M$ has been used as the measure of error variance.

Therefore, the total variance of response at generation t can be expressed as:-

$$V(R_t) = 2\sigma^2[th^2(1-h^2)/N + (t-1)h^4/M + (1-0.5\ h^2)/M]$$

By defining the proportion selected as $p = N/M$ and collecting terms, the more common expressions derived by Hill (1971, 1972, 1980) can be easily derived.

The covariance between responses observed at two generations contains the drift variance present at the earlier of the two generations. In addition, there is a covariance between the selection differentials and the response observed at the earlier generation. This additional covariance was assumed to be $h^2\sigma^2/M$ arising from the variance about the mean (σ^2/M) and the genetic regression (h^2) (Hill, 1971). It is likely that this expresssion should also depend on the family structure but the simplified form has been used. Thus, the covariance between responses observed at generations (t) and (T), where $t < T$, can be written as:-

$$\mathrm{cov}(R_t,\ R_T) = 2\sigma^2[th^2(1-h^2)/N + (t-1)h^4/M + h^2/M]$$

We now need to extend the model to allow for two sexes, with different proportions of animals selected in each sex, and for overlapping generations. Details of the appropriate formulations can be found in Johnson (1977). Briefly, we first define a matrix, P, which contains the expected proportions of genes in male and female progeny derived from various parental age groups, and off-diagonal elements representing ageing of parents. The structure of this matrix is described by Hill (1974). A further diagonal matrix, W_t, defines the expected increments in drift variance at time (t). For progeny born at time (t) the drift variances are those defined previously. There are also small increments in variance for parental groups since some individuals die before the end of their reproductive life (see Johnson, 1977). The cumulative drift at time (t+1) is then a function of cumulative drift up to time (t) plus the incremental drift at time (t), viz:-

$$Z_{(t+1)} = PZ_t P' = W_t$$

where Z = drift variance matrix

The variance of response for progeny born at time (t) can be found from the matrix, Z_t and the relevant row of the P matrix for the drift variance, to which can be added the appropriate error variance. Similarly, covariances between responses at different times can be determined as described by Johnson (1977).

Direct responses to selection

In order to estimate a variance-covariance matrix of responses, certain flock structure parameters are required including:-

- number of animals (of both sexes) recorded in each year
- number of animals selected
- numbers in each parental age group
- proportion of genes in progeny which are derived from each parental age group. This will reflect not only relative numbers in the parental age groups but also differential fertility

Average values for these parameters across selection lines are shown in Table 5.8. Variation between years within lines was very small and, since the variation between lines was also small, Table 5.8 contains some assumed values for a single idealised line that have been used to estimate the variance-covariance matrix of direct

Table 5.8. Population parameters for the CONTROL and selected lines (LONG and SHORT).

	Flock			
	CONTROL	LONG	SHORT	Assumed value
Animals recorded per year				
- males	98	100	93	100
- females	100	103	98	100
Animals selected per year				
- males	10.5	10.3	10.2	10.3
- females	69	70	68	69
Adult ewes of each age				
- 2 years	65	65	62	64
- 3 years	60	61	60	60
- 4 years	55	55	55	55
- 5 years	50	50	50	50
- 6 years	37	36	42	38
Proportion of genes in progeny from parental age classes:-				
- sires (1 year)	0.5	0.5	0.5	0.5
- dams - 2 years	0.096	0.096	0.094	0.095
- 3 years	0.115	0.112	0.111	0.112
- 4 years	0.114	0.115	0.113	0.114
- 5 years	0.101	0.102	0.103	0.102
- 6 years	0.074	0.075	0.079	0.077
Proportion of genes in selected sires from parental age classes:-				
- sires (1 year)	0.5	0.5	0.5	
- dams - 2 years	0.071	0.089	0.066	
- 3 years	0.111	0.131	0.136	
- 4 years	0.144	0.119	0.134	
- 5 years	0.108	0.091	0.104	
- 6 years	0.066	0.070	0.060	

response (V-matrix).

The estimate of realised response to selection was the regression of cumulative response on cumulative selection differential where both variables represented the divergence between the LONG and SHORT lines. Initially, an unweighted regression was estimated which gave a realised heritability of 0.503±0.004. Hill (1972a) developed an approximate variance of a realised heritability based on asymptotic drift formulae. Using this approximation, the standard error of the realised heritability was ±0.0207, which could be thought of as a first-order approximation. Using the variance-covariance matrix, a generalised least-squares solution of realised heritability was obtained from:-

$$b = (X'V^{-1}X)^{-1}X'V^{-1}Y$$

where b = realised heritability

X = vector of cumulative selection differentials

Y = vector of cumulative responses

V = variance-covariance matrix of responses

An initial estimate of heritability from the unweighted regression was used to generate the variance-covariance matrix and a new estimate of the regression coefficient obtained. The procedure was then iterated using the new estimate until convergence. The generalised least-squares estimate of the realised heritability was 0.489±0.0220.

It is clear that, in these data, ignoring the increasing variance of the responses with time and the correlations between responses substantially underestimated the variance of the realised regression. The inclusion of a more appropriate estimate of the variance with overlapping generations had only a small influence on the variance of the regression. A clearer perspective on the standard errors of the realised heritability is provided by Figure 5.4 in which the regressions and their standard errors were estimated progressively throughout the experiment, including each year successively into the model. Initially, the regression estimates and their standard errors were variable but two important issues quickly emerged:-

(i) Although the approximation for discrete generations (Hill, 1972a) and the overlapping generations procedure (Johnson, 1977) were asymptotically similar, they were very different from each other in the early years of the experiment. The reason for this can be seen from Table 5.9 in which the estimated drift variances at each year of the experiment are compared with the estimated asymptotic rate of drift. As observed by Johnson (1977), the initial rate of drift in a population with overlapping generations was higher initially but stabilised to a fixed increment above the asymptotic rate. This equilibrium point is obviously dependent on the number of parental age classes in each sex and the age at which males and females are first used for breeding progeny.

(ii) The impact of including a variance-covariance matrix for the response can be gauged from the ratio of the 'true' (generalised least squares) to 'apparent' (ordinary least squares) standard errors of regression. This ratio increased from 1.1 at year 2 to 5.9 at year 19 of the experiment.

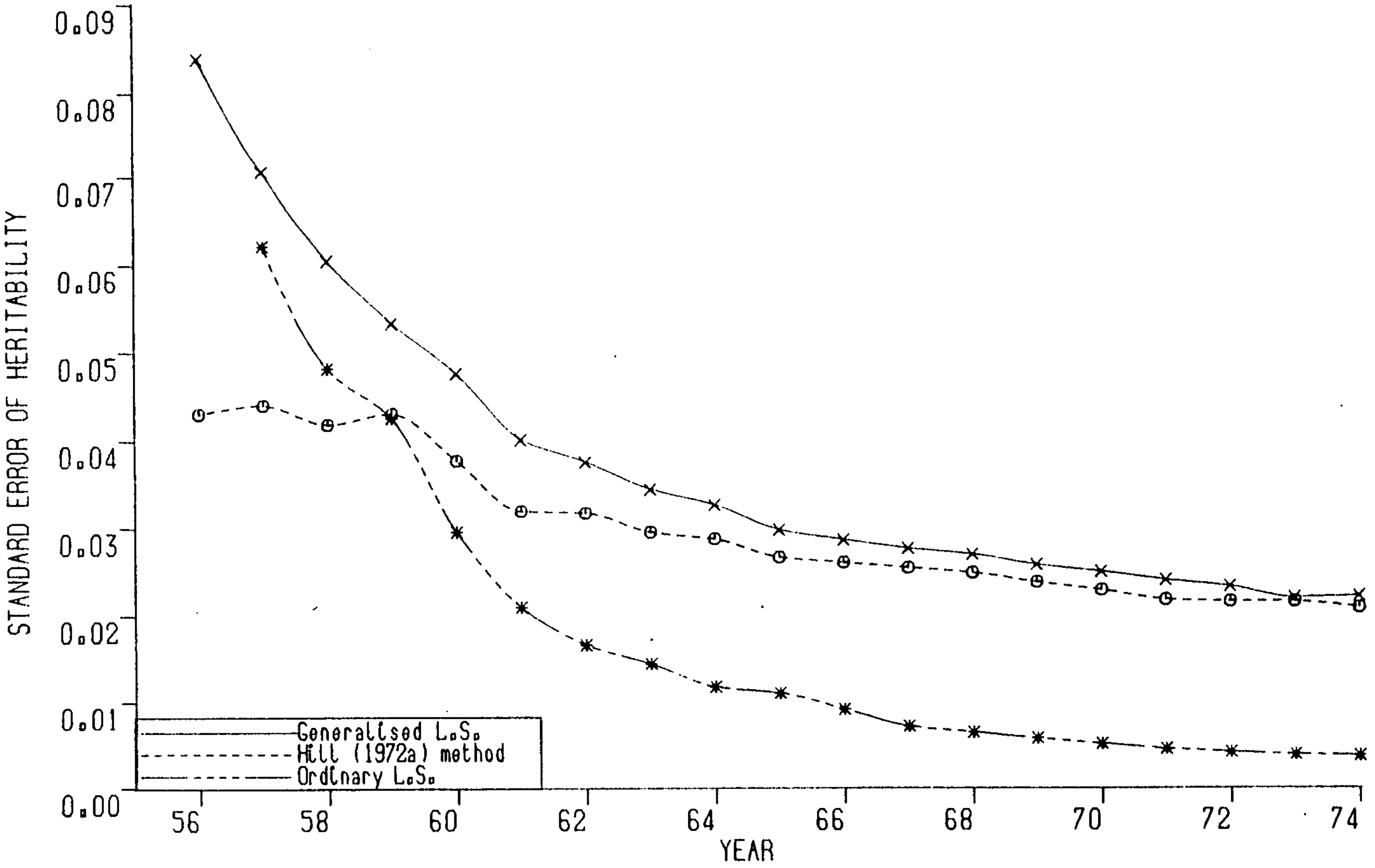

FIGURE 5.4. Apparent precision of realised heritability by three months.

<u>Table 5.9</u>. Estimated drift variance for cumulative responses in COR in each year for (i) asymptotic rates and (ii) the merhod of Johnson (1977).

Year	Cumulative response (cm)	Expected drift variance ($cm^2 \times 10^4$):-	
		(i) Asymptotic rate	(ii) Johnson method
1956	0.40	4	24
1957	0.46	9	31
1958	0.58	13	34
1959	0.49	17	38
1960	0.71	21	42
1961	0.97	25	47
1962	0.97	30	52
1963	1.07	34	57
1964	1.24	38	62
1965	1.29	44	66
1966	1.52	46	70
1967	1.52	50	74
1968	1.62	55	79
1969	1.75	59	83
1970	1.95	63	87
1971	2.11	67	91
1972	2.13	71	95
1973	2.23	75	100
1974	2.29	79	104

Correlated responses to selection

In the same manner as before we can define a variance-covariance matrix for the observed correlated responses, conditional on the observed selection differentials for the directly selected trait. For each of the direct and correlated traits (X and Y respectively) we have a heritability (h^2) and a phenotypic variance (σ^2), and a genetic correlation (r) between the traits. Then, the variance of the correlated response at generation (t), from Hill (1971) , is:-

$$V(C_t) = 2\sigma_y{}^2[th_Y{}^2(1-r^2h_X{}^2)/N+(t-1)h_Y{}^2h_X{}^2r^2/M+(1-0.5_r{}^2h^2{}_y/M]$$

Similarly, the covariance between correlated responses observed at generations (t) and (T), where t<T, is:-

$$Cov(C_t, C_T) = 2\sigma_Y{}^2[th_Y{}^2(1-r^2h_X{}^2)/N+(t-1)h_Y{}^2h_X{}^2r^2/M+ r^2h^2{}_y/M]$$

Combining these expressions with the methodology of Johnson (1977), the appropriate V-matrix could be derived using the base population estimate of heritability for the correlated trait (from Chapter 4) and an initial value for r from an unweighted analysis of realised correlated responses. Again, an iterative generalised least-squares solution was obtained for the regression of cumulative response in the correlated trait on cumulative selection differential in the directly selected trait.

Two-trait selection objective

We can also extend the previous approach for direct response to selection on a single trait to responses in two traits selected simultaneously. Berger and Harvey (1975) gave an account of a procedure for estimating realised heritabilities and genetic correlations from a two-trait selection programme. A major difficulty with this procedure is that standard errors of the realised genetic parameters cannot be derived (Berger, 1977). I am indebted to R. Thompson (pers. comm.) for deriving the appropriate variance-covariance matrix of responses so that standard errors of realised parameters can be estimated.

Firstly there is a vector of observed cumulative selection differentials at each year for both selected traits (S_1 and S_2) in absolute units. The effective weight applied to each trait in standard deviation units (vectors A_1 and A_2) can be found from:-

$$\begin{bmatrix} P_{11} & P_{12} \\ P_{21} & P_{22} \end{bmatrix} \begin{bmatrix} A_1 \\ A_2 \end{bmatrix} \begin{matrix} = \\ = \end{matrix} \begin{bmatrix} S_1 \\ S_2 \end{bmatrix}$$

where P_{11} = phenotypic variance of trait 1

P_{12} = phenotypic variance of trait 2

P_{22} = phenotypic covariance between traits 1 and 2

Then, the vectors of responses in the two traits (R_1 and R_2) can be used to estimate the genetic variances for the two traits (G_{11} and G_{22}) and the genetic covariance between them (G_{12}):-

$$\begin{bmatrix} A_1 & A_2 & 0 \\ 0 & A_1 & A_2 \end{bmatrix} \begin{bmatrix} G_{11} \\ G_{12} \\ G_{22} \end{bmatrix} = \begin{bmatrix} R_1 \\ R_2 \end{bmatrix} \quad \text{i.e. } A\,G = R$$

By including a variance-covariance matrix for the responses (V), a generalised least squares selection for the genetic variance-covariance (matrix G) can be derived from

$$G = (A' V^{-1} A)^{-1} A'V^{-1}R$$

The variance-covariance matrix of the responses was derived in the same way as the variance-covariance matrix for direct responses previously except that the scalars σ^2, $h^2\sigma^2$ and $h^4\sigma^2$ in the equations were replaced by 2x2 matrices of P, G and $G'P^{-1}G$ respectively where the diagonal elements of each matrix were the variances for traits 1 and 2 and the off-diagonal elements represented the covariance between the two traits. Again, the process could be iterated until convergence was reached.

It is critical to appreciate the conditions under which two-trait selection actually provides information on all three parameters (G_{11}, G_{12} and G_{22}). If the selection differentials for trait 2 are a function of those for trait 1, the vector of selection differentials in each year collapses to a scalar and the experiment is merely a single-trait selection experiment. For example, if selection is on a fixed index of traits 1 and 2, the observed selection differentials for the index contains all the information available. So a two-trait selection analysis is only relevant to an experiment where two lines were selected on different combinations (or indexes) of the two traits. The relative amount of information provided on each trait is a function of the difference in magnitude of the index weights between the two lines (Gunsett, Andriano and Rutledge, 1984). In the LONG and SHORT lines in this experiment, selection was applied on both COR and WT independently. The primary trait, COR, was selected in opposite directions (or equal and opposite index weights) while WT was included with retrospective index weights that were of the same sign but slightly different magnitude (Figures 5.3). Thus we could predict that a two-trait analysis of the experiment should provide precise information on response in COR but relatively imprecise information for WT.

CHAPTER 6

A GENETIC ANALYSIS OF THE COMPONENTS OF LIFETIME PRODUCTIVITY PRODUCTIVITY

INTRODUCTION

An important objective of the experiment was to estimate correlated responses in characters of commercial importance in hill sheep. In order to interpret any such responses in terms of genetic correlations we must first estimate genetic variances for these characters. In this chapter we examine genetic variation that exists in unselected Scottish Blackface sheep for commercially important traits. These analyses will also provide genetic and phenotypic parameters required to develop appropriate breeding plans for the economic improvement of Blackface sheep in hill environments.

The important components of lifetime productivity of hill sheep have been broadly defined as ewe survival, reproductive performance, body growth from birth to maturity and wool production. The data set used was restricted to the unselected BASE and CONTROL flocks so as to minimise selection biases on parameter estimates. Some preliminary estimates of genetic parameters for reproductive performance from the same population have been reported previously by Purser (1965).

MATERIALS AND METHODS

(i) Sheep and Management

The sheep and their management have been described in detail in Chapter 3. In particular, the procedures used for mating and lambing of the ewe flock are detailed on pages 39 - 42.

(ii) Measurements

Reproductive performance and ewe survival

Ewes selected to enter the breeding flock were first mated at about 18 months of age to lamb at 2 years of age. Surviving ewes remained in the breeding flock for five successive annual matings (or parities) or until they were considered incapable of rearing a lamb in the ensuing year. At each parity ewes were classified according to whether they survived to the next parity or not. No distinction was made between deaths or necessary culling among ewes not surviving.

The reproductive performance of each ewe in each year was partitioned into a number of components for analysis:-

lambed or not (fertility)
number of lambs born (litter size)
number of lambs weaned per lamb born (lamb survival)

Fertility. Since ewes were mated to a single ram in any year, the probability of lambing was a function of both the ewe and the ram. The inclusion of matings by chaser rams substantially reduced the variation between mating groups so that fertility was more appropriately a trait of the ewe with diminished influence of variation in ram fertility.

Litter size. Litter size was defined as the number of lambs produced by a ewe at birth, whether born alive or dead.

Lamb survival. Due to the practice of fostering, it was impossible to define the trait of lamb survival as a trait of the ewe. The best compromise was to assume that all lambs fostered would not have survived to weaning had they been left with their natural dams. This assumption underestimates both the actual survival rate (since about 60 percent of all fostered lambs were successfully reared to weaning), and also, probably, the likely survival rate had no fostering been practiced. There was no feasible alternative since foster dams were chosen without regard to selection line or age of the ewe.

Body weights

Body weights were recorded at various stages throughout the animal's life. The weights analysed in this paper were coded for the approximate age, in months, of the animal at weighing and were recorded at the following times:-

W0 - weight of each lamb within 24 hours of birth

W2 - weight on a single day when the average age of all lambs was about 56 days. This weight corresponded with the measurement of cannon bone length.

W4 - weight at weaning. All lambs in each year were weaned at one time. The average age at weaning ranged from 105 to 116 days between years with an overall mean of 111 days

W6 - recorded in October prior to the onset of winter

W12 - recorded in April, during early spring

W14 - recorded in June at the time of hogget sheering.

W16 - recorded in August

W18, W30, W42, W54, W66 -recorded in October-November prior to the commencement of first, second, third, fourth and fifth matings respectively

Fleece weights

All ewes were first shorn in June when 14 months of age (hogget fleece). Thereafter ewes were clipped annually in June of each successive year at approximately 2, 3, 4, 5 and 6 years of age. Ewes that had shed part or all of their fleece were noted and the weight of each fleece shorn was recorded at shearing. Records of fleece weight for all ewes with a whole fleece at shearing were analysed.

(iii) Records available

Data were available for lambs born between 1954 and 1974 inclusive within a base flock (1954-55) and a random-bred control flock (1956-74). Body weights up to weaning were available on all animals. Post-weaning and hogget body weights and hogget fleece weights were available for ewes born between 1954 and 1972 only. Adult records were available up to the 1973 year of observation only. Therefore, first parity records (W18, first parity reproductive components, 2 year old fleece weight) were available for ewes born between 1954 and 1971, second parity records for ewes born between 1954 and 1970, and so on up to fifth parity records for ewes born between 1954 and 1967 only. The approximate numbers of ewe records available at various ages, according to year of birth, are shown in Table 6.1.

(iv) Statistical analysis

The significance of certain fixed effects was first tested

<u>Table 6.1</u>. Numbers of ewe records available at various ages, according to year of birth.

Year of birth	Numbers of surviving ewes with records available at:-							
	Birth*	Weaning	Hogget (14 months)	Parity 1 (2 years)	Parity 2 (3 years)	Parity 3 (4 years)	Parity 4 (5 years)	Parity 5 (6 years)
1954	390	229	194	192	180	170	144	98
1955	433	302	251	252	238	221	196	165
1956	103	95	65	63	60	53	45	36
1957	122	108	75	74	68	60	55	42
1958	102	93	69	66	59	57	50	43
1959	138	121	68	69	62	56	52	48
1960	119	101	59	57	54	52	50	43
1961	111	94	67	66	60	52	48	34
1962	118	101	59	58	52	49	47	34
1963	127	109	62	64	60	56	51	40
1964	115	92	61	66	64	60	54	39
1965	132	97	58	55	51	48	43	27
1966	94	75	59	57	53	50	48	29
1967	108	93	59	57	51	50	41	24
1968	128	105	71	69	66	60	53	-
1969	120	96	69	69	66	58	-	-
1970	107	94	69	69	61	-	-	-
1971	114	97	71	70	-	-	-	-
1972	114	100	70	-	-	-	-	-
1973	113	99	-	-	-	-	-	-
1974	128	113	-	-	-	-	-	-
TOTAL	3036	2414	1556	1473	1305	1152	977	702

*An equivalent number of male records were available for birth weight and weight at 2 months of age.

for each body weight, fleece weight or reproduction component at each parity. These fixed effects were fitted within sires and included effects for hirsel, age of dam (2, 3, 4 5 or 6 years of age), birth/rearing type (single/single, twin/single, or twin/twin) and age of animal (both linear and quadratic regressions). A further fixed effect for first winter treatment was also fitted since some animals in some years were wintered away from the hill. This practice was undertaken for animals born between 1954 and 1959, with some ewes always remaining on the hill and others wintered away in 1, 2, 4, 7 or 9 separate locations depending on year. Winter treatment was treated as a fixed effect nested within year of birth. Non-significant ($p>0.05$) effects were successively omitted from the models and the reduced models refitted for each variable.

The basic data set was adjusted for significant fixed effects before the genetic analyses were undertaken. This was done because some analyses, particularly analyses of covariance, were made on parts of the data set and because different fixed effects were of importance at different ages. Therefore, rather than explicitly fit all fixed effects in each analysis, each trait was first adjusted for the important fixed effects appropriate to that trait from the complete data set, and all subsequent analyses were performed on the adjusted data set.

Heritabilities and genetic correlations were estimated by paternal half-sib components of variance. All data available for each trait were used to estimate heritability. Genetic correlations were estimated for each pair of traits and all animals with observations on both traits were used. Maternal half-sib correlations were estimated from between-dam components of variance. Where full-sibs were present, one was drawn at random for inclusion in the analysis and the other excluded. Additionally, any fostered lambs were excluded from maternal correlation analyses. Standard errors of heritabilities, genetic correlations and maternal correlations were estimated as linear functions of the variance and covariance components (Becker, 1975).

RESULTS

(i) Ewe survival

The survival of ewes from year to year can be followed approximately in Table 6.1. There was an annual loss of ewes of between 7 and 12 per cent after each of the first three parities, and a further loss of 25 per cent after fourth parity. The effect of previous performance on whether or not a ewe survived is shown in Table 6.2 for the major traits of lifetime productivity. Barren ewes were more likely to be culled than ewes lambing previously and this effect was significant at all parities, although smaller in first parity ewes. From an analysis of binomial proportions using GLIM (Baker and Nelder, 1978), the predicted proportions of ewes culled for previously lambing ewes were 0.06, 0.05, 0.09 and 0.23 at parities 1 to 4 respectively, while the comparable proportions for barren ewes were 0.11, 0.24, 0.27 and 0.36 respectively. Over all parities, surviving ewes also tended to be heavier (Table 6.2), but this effect was probably related to the culling on barrenness since it will be shown that barren ewes were lighter. Genetic parameters for barrenness (or its complement, ewes lambing) could be biassed by this culling but the effects on the other traits should be small.

Table 6.2. Differences between culled and surviving ewes based on previous year's performance. Culling effects were estimated separately at each parity and then pooled across parities.

Trait	Mean performance of surviving ewes	Performance of culled ewes as a deviation from surviving ewes (± standard error)
Litter size per ewe lambing	1.082	0.017±.015
Ewes lambing per ewe mated	0.878	-0.151±.015
Body weight (kg)	40.59	-0.97 ±.21
Fleece weight (kg)	1.507	-0.034±.022

In Table 6.3 are presented heritability estimates for both survival in separate parities and for cumulative survival. Although the estimates have large sampling variances, they suggest some additive genetic variation particularly after fourth parity when ewes were commonly culled for broken mouths and udder faults.

(ii) Reproductive performance

Age effects on reproductive performance are shown in Table 6.4. Parities 1 to 5 correspond to lambing at age 2 years to 6 years respectively. First parity ewes had significantly lower fertility, litter size and lamb survival than later parities. Differences between later parities were small although ewe fertility was apparently declining in late parity ewes.

Age of dam, birth type, date of birth, hirsel or winter treatment were never significant sources of variation in analyses of reproductive components for individual parities. Though not significant, ewes born as twins produced larger litters at all parities than ewes born as singles. Genetic analyses of reproductive components were therefore undertaken on the observed data with no adjustment for any fixed effects.

Heritabilities were first estimated for each parity separately for each reproductive component, and genetic and phenotypic correlations between parities were then estimated. Estimates of heritability of ewe fertility, lamb survival (as a trait of the dam) and lambs weaned for individual parities were very low and between-sire variance components were commonly negative. The heritability of litter size was generally much higher and estimates for each parity are shown in Table 6.5, using all

Table 6.3. Heritability estimates for ewe survival at individual parities and for cumulative ewe survival

	Parity 2	Parity 3	Parity 4	Parity 5
Survival to parity i per ewe at parity (i-1)				
- mean	0.93	0.92	0.90	0.75
- heritability (±standard error)	0.19 ± .08	-0.02 ± .09	0.05 ± .09	0.24 ± .12
Cumulative survival to parity i per ewe at parity 1				
- mean	0.93	0.86	0.78	0.58
- heritability (±standard error)	0.19 ± .08	0.08 ± .08	0.02 ± .08	0.16 ± .09

Table 6.4. Age effects on the components of reproductive performance

Reproductive component	Age of ewe at lambing				
	2 years	3 years	4 years	5 years	6 years
Fertility - ewes lambing per ewe mated	0.815a	0.882c	0.893c	0.867bc	0.831ab
Litter size - lambs born per ewe lambing	1.030a	1.059b	1.115c	1.132c	1.125c
Lamb survival - lambs weaned per lamb born					
- single lambs	0.754a	0.876b	0.912c	0.907c	0.894bc
- twin lambs	0.389a	0.644b	0.675b	0.813c	0.719bc
Lambs weaned per ewe lambing	0.767a	0.895b	0.964c	0.992c	0.958c

Within a row, means followed by the same letter are not significantly different from each other (p>0.05).

Table 6.5. Heritability of litter size at each age

Parity	Full data set			Restricted data set (at least 3 ewes per sire)		
	No. of sires	Ewes/ sire	h^2(±se)*	No. of sires	Ewes/ sire	h^2(±se)*
Age of ewe at lambing						
- 2years (Parity 1)	255	4.54	0.11±0.09	206	5.30	-0.12±.10
- 3 years (Parity 2)	239	4.70	0.21±0.10	205	5.25	0.10±.09
- 4 years (Parity 3)	232	4.41	0.18±0.10	186	5.18	0.18±.10
- 5 years (Parity 4)	220	3.86	0.26±0.13	164	4.70	0.25±.12
- 6 years (Parity 5)	198	2.97	0.11±0.17	112	4.16	0.06±.15
Weighted average (Parities 1-5)			0.17±0.05			0.09±.05
Weighted average (Parities 2-5)			0.19±0.06			0.15±.05

*heritability (± standard error)

available data. Since the F-values for the between-sires source of variation in the analyses of variance were close to 1, the analyses were repeated after excluding all sires with less than three progeny. Robertson (1962) showed that when F-values approach 1, the component of variance for sires has a sampling variance $(1+C^2)$ times greater than if family size was balanced, where C is the coefficient of variation in family size. The effect of this restriction on the number of sires, average sire family size and heritability of litter size is illustrated in Table 6.5. It is clear that the estimates have a wide sampling distribution given the change in their values with the relatively mild restriction applied. This only indicates that the data set is far short of an optimum design for estimating genetic parameters of litter size. In particular, the small sire family size for a binomially distributed trait such as litter size with a relatively low frequency of twin births, renders any estimates of genetic parameters of very limited precision. The problem of inadequate design is even more pronounced when estimating genetic correlations between parities (Table 6.6). The majority of the correlations obtained from the whole data set were not estimable due to negative variance component for one of the individual parities. Using the restricted data set, only two genetic correlations were estimated. In addition, those estimates obtained had extremely large standard errors.

With the data set, as designed, an alternative method of estimating genetic parameters was attempted. The analytical model is described in Table 6.7. All data from all parities were included in the analysis. For lamb survival (overall), the fixed effects of litter size (single or twin) and litter size x parity

Table 6.6. Phenotypic and genetic correlations[*] between litter size at each parity.

	Parity 1	Parity 2	Parity 3	Parity 4	Parity 5
Parity 1		0.18	0.15	0.18	0.12
Parity 2	0.65±0.59		0.28	0.27	0.24
Parity 3	n.e.[+]	0.79±0.36		0.27	0.29
Parity 4	0.20±0.54	n.e.	0.39±0.41		0.25
Parity 5	n.e.	n.e.	n.e.	n.e.	

[*] Phenotypic correlations above the diagonal and genetic correlations (± standard error) below the diagonal.

[+] n.e. Not estimable due to negative variance components.

Table 6.7. Genetic analysis of reproductive components, pooled across parities.

Source of variation	Expected mean square for random effects
Year of birth	
Sires/year	$\sigma_W^2+k_2\sigma_B^2+k_3\sigma_S^2$
Ewes/sires	$\sigma_W^2+k_1\sigma_B^2$
Parity	σ_W^2

$$\text{Repeatability} = \frac{(\sigma_S^2 + \sigma_B^2)}{(\sigma_S^2+\sigma_B^2+\sigma_W^2)} \qquad \text{Heritability} = \frac{4\sigma_S^2}{(\sigma_S^2+\sigma_B^2+\sigma_W^2)}$$

K values

- litter size, lamb survival, lambs weaned

  $k_1 = 3.37$, $k_2 = 3.77$, $k_3 = 18.64$

- fertility

  $k_1 = 3.74$, $k_2 = 4.13$, $k_3 = 21.56$

interaction were also included at the within-ewe level. For such analyses to generate meaningful estimates of heritability and repeatability, there are at least two implicit assumptions:-

(i) Genetic correlations between parities are all unity for each component. In the light of other estimates from sheep populations for at least litter size, this is a realistic "a priori" assumption.

(ii) Variances between parities are equal. Since the variance of a binomially distributed trait is a function of the incidence, such equality will not exist. However, the greatest divergence from equality will occur in first parity observations. Therefore, analyses were performed on the whole data set and again on a reduced data set from which all first parity records had been removed.

Estimates of heritability and repeatability of the reproductive components pooled over all parities, and excluding first parity, are presented in Table 6.8. For litter size the pooled heritability estimates obtained were quite similar to the weighted average estimates from separate parities (Table 6.5). Thus, the assumption of unity genetic correlations would seem appropriate. Estimates of heritability for fertility and lamb survival as traits of the ewe indicate very little additive genetic variance available in these traits. The removal of first parity records had little effect on estimates of heritability for any trait.

All reproductive components showed some evidence of repeatability, although only litter size could be described as

Table 6.8. Repeatability and heritability estimates for reproductive components for all parities (1-5) and parities (2-5).

	All data		Parities 2-5	
	Repeatability (±se)	Heritability (±se)	Repeatability (±se)	Heritability (±se)
Fertility	0.10±0.01	0.01±0.03	0.14±0.02	0.01±0.03
Litter size	0.22±0.02	0.12±0.04	0.27±0.02	0.14±0.05
Lamb survival	0.06±0.01	-0.02±0.02	0.08±0.02	-0.01±0.03
Lambs weaned per ewe lambing	0.06±0.01	0.01±0.03	0.10±0.02	0.03±0.04

having a moderate estimate. The repeatability of first parity records for all components was very low resulting in an increased average repeatability for all traits when first parity records were removed from the data set (Table 6.8).

(iii) Body weights from birth to maturity

Least squares means for body weights of ewes at various ages are plotted in Figure 6.1. The pattern of growth illustrates the seasonal pattern of pasture production with rapid pre-weaning growth, a net weight loss over the first winter and then rapid hogget growth during the spring and summer of the ensuing year. The loss of weight during winter was also found in adult animals, but only pre-mating weights (autumn) are shown on the graph. The average effect of the practice of wintering away from the hill during the animal's first winter is also illustrated in Figure 6.1. There were, in fact, a population of winter treatments but the average effect only, is shown. The more favourable environments away from the hill resulted in some growth over the first winter, but this advantage was rapidly reduced once all ewes were returned to the hill in spring. By first mating, the advantage in body weight of away-wintering was very small, and virtually non-existent at later ages.

Mean body-weight and coefficient of variation at each age are presented in Table 6.9. Coefficients of variation were of a similar order (10-12%) for all weights after weaning, but were substantially higher for preweaning weights. Age of dam and birth/rearing type were significant sources of variation for all weights between birth and 30 months of age, and their effects are

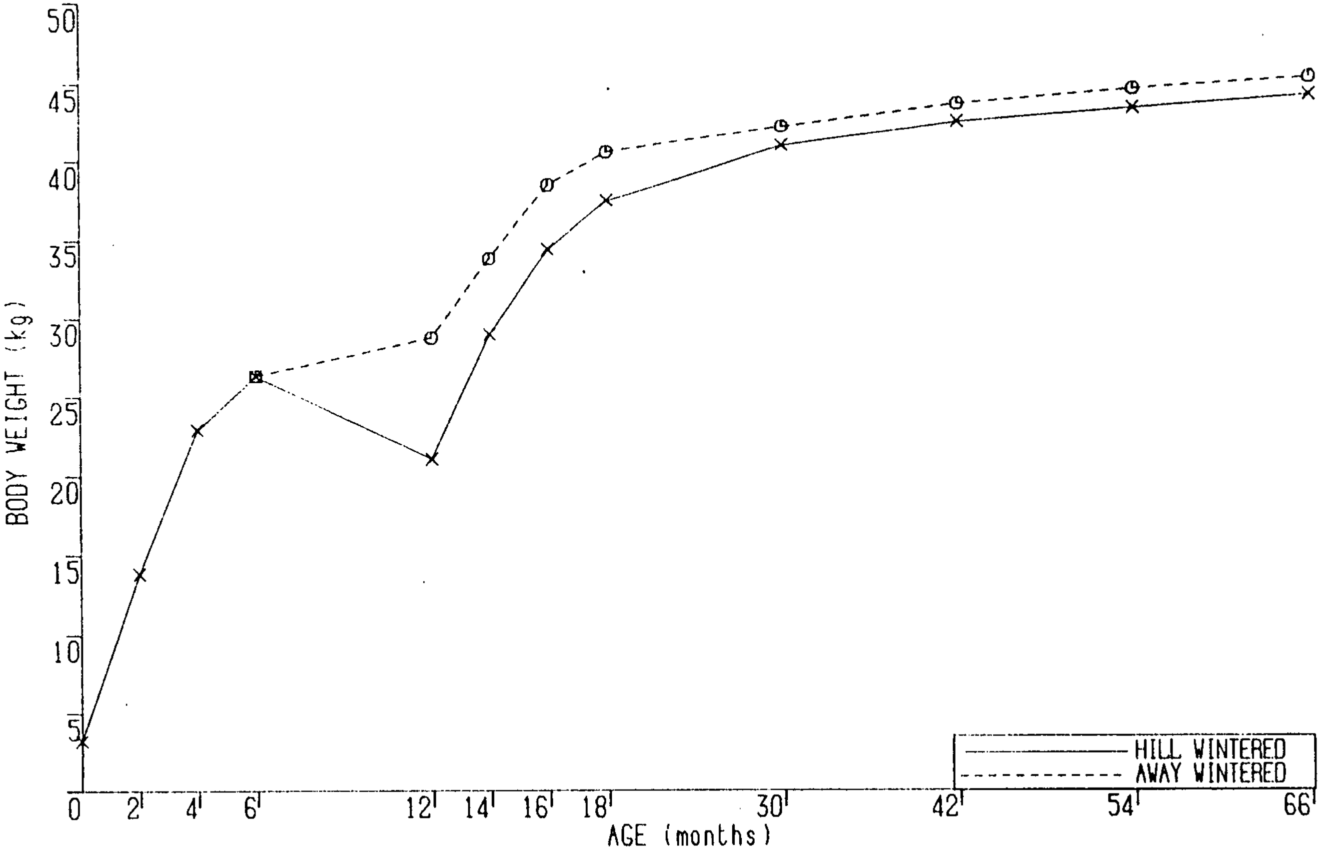

FIGURE 6.1. Average body weights of ewes from birth to 5 1/2 years of age.

Table 6.9. Means, coefficients of variation, heritabilities, maternal correlations and certain fixed effects for body weights of ewes from birth to maturity.

	Body weight (average age in months)											
	W0	W2	W4	W6	W12	W14	W16	W18	W30	W42	W54	W66
Mean (kg)	2.9	12.1	21.2	25.1	20.7	28.5	33.9	37.0	40.0	42.5	43.3	44.0
Coefficient of variation (%)	18.6	18.1	15.0	11.5	12.2	10.5	101	9.4	11.1	10.7	10.9	10.5
Heritability (paternal half sib) ± standard error	0.13 ±.03	0.07 ±.04	0.05 ±.04	0.25 ±.07	0.21 ±.08	0.15 ±.07	0.29 ±.09	0.33 ±.09	0.27 ±.10	0.28 ±.12	0.34 ±.12	0.36 ±.15
Maternal half-sib correlation±s.e.	0.35 ±.03	0.31 ±.03	0.32 ±.03	0.25 ±.05	0.31 ±.05	0.23 ±.05	0.18 ±.06	0.14 ±.06	0.21 ±.06	0.16 ±.07	0.10 ±.08	0.07 ±.10
Fixed effects*												
- age of dam												
2 years	-.73	-.72	-.72	.-56	-.36	-.32	-.33	-.30	-.22	-.14	-.09	-.16
3 years	-.22	-.15	-.12	-.20	-.15	-.13	-.10	-.08	-.04	-.09	-.02	.02
4 years	.17	.22	.15	.20	.18	.08	.08	.15	.06	.07	.01	.03
5 years	.36	.35	.37	.25	.18	.17	.19	.10	.09	0	.05	0
6 years	.42	.30	.32	.32	.14	.20	.16	.13	.18	.11	.13	.10
-Birth rearing type												
Single/single	.82	.43	.49	.36	.19	.19	.15	.13	.20	.02	-.01	.02
twin/single	-.82	-.18	-.07	-.03	-.04	.03	.10	.03	-.05	-.12	.02	.10
twin/twin	-.82	-.24	-.42	-.33	-.14	-.21	-.25	-.16	-.15	-.10	0	-.12

*Fixed effects expressed as least squares constants standardised by phenotypic standard deviation shown in Table 6.9 as least squares constants standardised by the phenotypic standard deviation appropriate to each weight. Increasing age of dam resulted in significantly increased body weight up to 5 years of age for preweaning weights and up to 4 years of age for post-weaning weights to W30. As would be expected, the influence of age of dam declined steadily after weaning. For example, the difference in body weight between lambs born to 2 year old dams and those born to 5 or 6 year old dams was more than one standard deviation (1σ) from birth to weaning, about 0.5σ at 12-16 months of age and about 0.35σ at 30 months of age. Although not significant, there was still a difference of about 0.2σ at weights recorded between 42 and 66 months of age. Similarly differences between ewes born as singles and those born and reared as twins declined with age from about 1.6σ at birth, to o.9σ at weaning, to about 0.4σ between 12 and 16 months of age and finally to zero between 42 and 66 months of age. On the other hand, the effect of variation in lamb age on body weight recorded on a single day was only a significant source of variation in weights recorded at 2, 4 and 6 months. During this period, the regression coefficient in standardised units declined rapidly from 0.046σ per day, to 0.021σ per day and to 0.013σ per day respectively.

Heritabilities for weights at each age, estimated by paternal half-sib components of variance, demonstrate evidence of change in genetic variance with age (Table 6.9). In particular, pre-weaning weights had a low heritability (less than 0.1) while weights at adult ages (W18-W66) were all consistently in the region of 0.3. The increase in the standard errors of the estimates with age reflect both declining numbers of sire families and declining numbers of ewe progeny per sire.

The intra-class correlation between maternal half-sibs showed a very consistent decline with increasing age (Table 6.9). The expectation of this maternal correlation is:-

$$t = (1/4\sigma_{Ao}^2 + \sigma_{Am}^2 + \sigma_{AoAm} + \sigma_{Em}^2)/\sigma_P^2$$

where σ_{Ao}^2 = direct additive genetic variance
σ_{Am}^2 = maternal additive genetic variance
σ_{AoAm} = direct-maternal additive genetic covariance
σ_{Em}^2 = maternal environmental variance
σ_P^2 = phenotypic variance

If there were no maternal effects (either genetic or environmental) the expectation of the maternal correlation would be one-quarter of the estimated heritability (paternal half-sib estimate). For W54 and W66 (Table 6.9), such was the case. For earlier weights particularly those recorded up to weaning, there was obviously a large effect of maternal genotype and/or maternal environment on an animal's performance. Age of dam and birth/rearing type are examples of specific maternal environmental effects that can influence an animal's growth. These specific effects persisted almost throughout the animal's production life. The maternal correlations indicate that there were other general (or non-specific) maternal effects operating, and it is noteworthy that these persisted over a similar period and in a similar declining fashion as the specific maternal environmental effects.

Genetic and phenotypic correlations between weights at various ages are presented in Table 6.10. The phenotypic correlations were quite precisely estimated and showed a high correlation between successive weights (0.6 to 0.9) and then declining values as the interval between weighings increased. Genetic correlations, with their higher sampling variances, were more variable. However, the estimates were less widely distributed than their individual standard errors would perhaps suggest. Excluding correlations involving birth weight, only 1 correlation of the 55 was not estimable due to a negative variance component 2 estimates were negative in sign, and of 18 estimates exceeding 0.8 only 3 exceeded the notional limit of 1.0. In general, genetic correlations between successive weights were higher and the decline with increasing interval between weights more pronounced than for corresponding phenotypic correlations.

To condense the results and facilitate interpretation, the parameter estimates have been pooled into five natural stages of growth, namely:-

- birth weight (W0)
- pre-weaning weights (W2, W4)
- post-weaning weights (W6, W12)
- hogget weights (W14, W16)
- adult weights (W18, W30, W42, W54, W66)

While the grouping was somewhat arbitrary, the genetic correlations between the grouped weights were not significantly different from unity. Pooled parameters were weighted by the inverse of their sampling variances and a pooled standard error computed.

Table 6.10. Phenotypic correlations (above the diagonal) and genetic correlations (below the diagonal) between body weights from birth to maturity.

	W0	W2	W4	W6	W12	W14	W16	W18	W30	W42	W54	W66
W0		.44	.40	.35	.28	.28	.30	.27	.22	.29	.22	.24
W2	.26 (±.24)		.86	.74	.52	.52	.50	.43	.31	.32	.29	.34
W4	-.77 (±.36)	1.02 (±.75)		.86	.62	.59	.60	.54	.43	.40	.37	.39
W6	-.07 (±.32)	.82 (±.15)	.88 (±.06)		.67	.65	.63	.60	.44	.42	.41	.44
W12	.26 (±.37)	.96 (±.24)	.76 (±.14)	.96 (±.10)		.74	.66	.64	.41	.42	.41	.41
W14	-.12 (±.41)	.30 (±.40)	.48 (±.13)	.67 (±.19)	.99 (±.11)		.83	.74	.45	.43	.43	.41
W16	.20 (±.28)	.29 (±.37)	.55 (±.19)	.62 (±.18)	.92 (±.12)	.91 (±.06)		.86	.55	.54	.52	.48
W18	-.14 (±.33)	-.15 (±.35)	.20 (±.24)	.49 (±.17)	.64 (±.15)	.86 (±.15)	.86 (±.06)		.60	.57	.54	.55
W30	-.12 (±.33)	.39 (±.44)	.64 (±.25)	.81 (±.17)	.80 (±.20)	1.00 (±.24)	.92 (±.13)	.97 (±.10)		.64	.64	.59
W42	-.07 (±.41)	0 (±.83)	.27 (±.38)	.47 (±.24)	.48 (±.25)	.73 (±.27)	.76 (±.16)	.90 (±.13)	1.06 (±.11)		.70	.64
W54	-.06 (±.35)	.11 (±.41)	.23 (±.30)	.29 (±.24)	.18 (±.33)	.42 (±.43)	.71 (±.27)	.70 (±.19)	.97 (±.12)	.90 (±.11)		.67
W66	.02 (±.34)	.27 (±.46)	.09 (±.42)	.32 (±.32)	-.13 (±.54)	.68 (±.24)	.76 (±.58)	n.e.	1.12 (±.38)	.76 (±.16)	.95 (±.16)	

+ n.e. = not estimable

The pooled estimates of genetic correlations (Table 6.11) indicated a marked degree of independence in the additive genetic effects influencing weight at particular ages. Birth weight was apparently genetically independent of body weight at any subsequent stage of development. Similarly, body weight up to weaning had a low genetic correlation with adult weight. Conversely, selection for increased weight at maturity would result in little change in size at birth and growth rate to weaning but moderate correlated changes in postweaning weights. From comparisons of phenotypic and genetic correlations it was clear that estimates of environmental correlations were much less widely distributed indicating that environmental effects on body weight at a certain stage of development were quite moderately correlated with such environmental effects at other stages of growth. Such correlations might be expected to be important under hill conditions where the ewes were hefted to particular locations on the farm (Chapter 3).

Assuming genetic correlations of unity and equal variances pooled heritability and repeatability estimates for premating body weights over all five parities were made using the model described in Table 6.7. The pooled heritability estimate was 0.29 ± .04 compared with a weighted average estimate for the five weights of 0.31 ± .05. The estimated repeatability of premating body weight was 0.56 ± .02. Excluding first parity records (that is, weight at 18 months of age) had no effect on heritability and increased the repeatability estimate to 0.61 ± .03.

(iv) Fleece weights

Mean fleece weights for ewes kept on the hill are shown in

Table 6.11. Genetic and phenotypic parameters for pooled weight groups

	Birth weight	Preweaning weight	Postweaning weights	Hogget weights	Adult weights
Heritability	.13±.03	.06±.03	.23±.05	.21±.06	.31±.05
Maternal repeatability	.35±.03	.32±.04	.28±.03	.21±.04	.15±.03
Correlations*					
Birth weight		.42	.31	.29	.25
Preweaning weights	-.07±.20		.69	.55	.38
Post-weaning weights	.06±.24	.86±.05		.67	.46
Hogget weights	.10±.23	.47±.13	.87±.07		.54
Adult weights	-.08±.16	.26±.11	.56±.07	.85±.05	

*Phenotypic correlations above the diagonal and genetic correlations (± standard error) below the diagonal.

Table 6.12. The practice of wintering away from the hill during the animal's first winter increased hogget fleece weight by an average of 0.31kg, but had no significant effect on adult fleece weight. These means do not represent true age effects on fleece weight for two reasons. Firstly, the interval to hogget shearing was, on average, 14 months from birth while for adult shearings the interval was only 12 months. Secondly, as will be shown later, reproduction level influenced fleece weight sbstantially so that adult fleece weight means were reduced by the effects of pregnancy and lactation. Adjusting for these influences, the approximate means for the weight of fleece produced annually by non-pregnant, non-lactating ewes would be 1.31, 1.70, 1.74, 1.69 and 1.58kg for ewes shorn at 1, 2, 3, 4, 5 and 6 years of age respectively.

Age of dam and birth/rearing type significantly influenced all fleece weights up to 5 year old and 3 year old fleeces respectively. The difference between ewes born to 2 year old dams and those born to 5 or 6 year old dams was 0.5σ for hogget fleece weight, 0.4σ for 2 and 3 year old fleece weights and 0.25σ for 5 year old ewes (Table 6.12). Differences between ewes born as singles and those born and reared as twins declined from 0.7σ for hogget fleece weight to less than 0.2σ for 3 year old fleece weight and were thereafter not significantly different from zero (Table 6.12). The effect of variation in age of ewe at shearing was only significantly different from zero from hogget fleece weight, the regression coefficient being 0.015σ per day.

Coefficients of variation and heritabilities for fleece weight at different ages were very similar and showed no evidence of

Table 6.12. Means, coefficients of variation, heritabilities, maternal correlations and certain fixed effects for lifetime fleece weights.

	Hogget fleece weights	Adult fleeces shorn at:-				
		2 years	3 years	4 years	5 years	6 years
Mean (kg)	1.49	1.67	1.48	1.45	1.41	1.31
Coefficient of variation (%)	23	25	27	26	26	28
Heritability (paternal half-sib) ± se	0.49 ±.09	0.55 ±.10	0.46 ±.10	0.42 ±.11	0.57 ±.13	0.64 ±.17
Maternal half-sib correlation ± se	0.16 ±.05	0.11 ±.06	0.10 ±.07	0.02 ±.08	0.07 ±.09	0.16 ±.11
Fixed effects*						
- Age of dam						
2 years	-.36	-.26	-.26	-.16	-.13	-.04
3 years	-.10	-.10	-.05	-.12	-.15	-.13
4 years	.15	.05	0	0	.07	-.10
5 years	.17	.15	.11	.14	.07	.21
6 years	.14	.16	.20	.13	.15	.06
- Birth/rearing type						
single/single	.37	.17	.16	.10	.05	-.03
twin/single	-.06	-.14	-.18	-.17	0	.02
twin/twin	-.31	-.04	.01	.06	-.05	.02

*Fixed effects expressed as least squares constants standardised by phenotypic standard deviation.

changes with age (Table 6.12). The average coefficient of variation was about 25 percent and average heritability about 0.5. Estimates of maternal half-sib correlations showed no evidence of large maternal genetic or maternal environmental effects on fleece weight. In fact, for adult fleece weights, the maternal correlation estimates were never more than one-quarter of the paternal half-sib heritability estimates.

Genetic and phenotypic correlations between fleece weights at various ages are presented in Table 6.13. Phenotypic correlations between successive fleece weights increased with age, while phenotypic correlations between pairs of fleece weights declined with increasing age interval between them. Genetic correlations were, in general, very high and had reasonably low standard errors. Genetic correlations between fleece weights recorded at 3, 4, 5 and 6 years of age were not significantly different from unity while some individual correlations involving hogget and 2 year old fleece weight did differ from unity. Weighted average estimates for the genetic correlations between hogget fleece weight and 3-6 year old fleece weights, and between 2 year old and 3-6 year old fleece weights were 0.79 ± .06 and 0.85 ± 0.04 respectively.

Estimates of pooled heritability and repeatability for adult fleece weights were 0.44 ± .06 and 0.59 ± .03 respectively. The weighted average of the heritability of individual adult fleece weights (Table 6.12) was 0.51 ± .05. Excluding first parity records (that is, 2 year old fleece weight) gave estimates of 0.45 ± .07 and 0.62 ± .03 for pooled heritability and repeatability respectively.

Table 6.13. Phenotypic correlations (above the diagonal) and genetic correlations (below the diagonal) between lifetime fleece weights.

Fleece weight at age:-	Fleece weight at :-					
	Hogget	2 years	3 years	4 years	5 years	6 years
Hogget		0.57	0.50	0.47	0.49	0.38
2 years	0.87 ±.07		0.66	0.61	0.61	0.54
3 years	0.85 ±.09	0.84 ±.07		0.69	0.63	0.58
4 years	0.79 ±.12	0.96 ±.08	1.04 ±.07		0.71	0.64
5 years	0.84 ±.11	0.81 ±.08	1.02 ±.07	1.07 ±.08		0.72
6 years	0.30 ±.20	0.62 ±.15	0.83 ±.13	0.98 ±.15	0.88 ±.08	

(v) Correlations among measures of lifetime productivity

Using the model described in Table 6.7, estimates of the correlations of litter size with body weight and fleece weight, of fertility with body weight and fleece weight, and of body weight with fleece weight were made. Genetic (from sire variance components, within-ewe (from records variance component) and phenotypic correlations were estimated for each pair of traits.

It has already been shown that including first parity records for the individual adult traits had no great effect on heritability, and the same was true for the correlation estimates. Thus, only the results polled over all parities have been included in Table 6.14.

There was no evidence of any genetic association between reproductive components and fleece weight (Table 6.14). For adult fleece weights, there was no genetic association with body weight although as hoggets the genetic correlation was moderate. The most important genetic correlation was that between litter size and body weight. The estimated correlation was 0.66, and even when first parity records were ignored the estimate was 0.63.

A common feature of the estimated correlations was the disparity between genetic and phenotypic correlation, probably indicating the presence of environmental influences that behave in a dissimilar manner to the genetic effects. Estimates of environmental correlations are generally imprecise, relying as they do on estimates of heritabilities and genetic correlation. In these data, the within-ewe correlations, while not exactly equivalent to environmental correlations, were totally environmental in origin. The genetic, phenotypic and within-ewe regressions of

Table 6.14. Correlations between reproductive traits, body weights and fleece weights

Traits		Genetic correlation(±se)	Phenotypic correlation	Within-ewe correlation
Fertility	Adult body weight	-0.17±.26	0.05	0.22
Litter size	Adult body weight	0.66±.18	0.20	0.14
Fertility	Adult fleece weight	-0.09±.29	-0.25	-0.32
Litter size	Adult fleece weight	-0.06±.15	0.01	0
Adult body weight	Adult fleece weight	-0.06±.10	0.24	0.14
Hogget body weight (W14)	Hogget fleece weight	0.40±.21	0.33	-

reproductive performance and fleece weight on mature body weight are presented in Table 6.15. These regressions represent the expected effect on performance of a unit change in body weight at the following levels of sampling:-

*genetic. Predicted correlated change in performance arising from a 1kg genetic response in body weight.

*phenotypic. Predicted change in current generation performance arising from choosing ewes whose average phenotype for body weight was 1kg greater than the mean weight.

*within-ewe. Predicted change in performance arising from a 1kg environmental change in the body weight of an individual ewe.

A genetic increase of 1kg in mature body weight would result in a large increase in litter size of 0.027 lambs born per ewe lambing but little change in ewe fertility or fleece weight (Table 6.15). In relative terms, the expected proportional change in mean litter size was equivalent to the proportional response in body weight itself. The implication of this genetic regression in terms of direct and indirect selection will be discussed later. At the within-ewe level, a 1kg increase in body weight would result in a relatively smaller increase in litter size (0.012 lambs born per ewe lambing) but larger increases in ewe fertility and fleece weight. In particular, the probability of a ewe lambing was very sensitive to any environmental fluctuation in body weight. This relationship did show some evidence of curvilinearity with

Table 6.15. Regressions of reproductive traits and fleece weight on adult body weight. Estimated correlated change in each trait arising from a 1kg increase in body weight at the genetic, phenotypic and within-ewe levels.

Trait	Mean	Predicted correlated change in trait per 1kg increase in body weight:-		
		Genetic	Phenotypic	Within-ewe
Fertility (ewes lambing per ewe mated)	0.858	-0.003	0.003	0.024
Litter size (lambs born per ewe lambing)	1.092	0.027	0.013	0.012
Fleece weight (kg)	1.46	-0.004	0.022	0.012

progressively smaller increases in fertility with increasing weight although the quadratic regression coefficient was not significant ($P = 0.10$).

The within-ewe relationship between reproductive components and fleece weight was examined explicitly by creating a dummy factor for analysis which included the various reproductive components as different levels, viz:-

0 - barren ewe

1 - single bearing ewe, no lambs reared

2 - single bearing ewe, lamb reared

3 - twin bearing ewe, no lambs reared

4 - twin bearing ewe, one lamb reared

5 - twin bearing ewe, two lambs reared. It is important to note that these ewes was managed separately after lambing until weaning.

The effect of reproductive level on fleece weight was then estimated in a model in which ewe identity was absorbed and the effects of parity and parity x reproductive level were also fitted. There were no significant differences between single and twin bearing ewes rearing no lambs, or between single and twin bearing ewes rearing one lamb, so these categories were pooled. The effect of reproductive level on fleece weight is shown for each parity in Table 6.16. As might be expected barrenness resulted in significantly greater weight of wool produced this advantage being similar at all parities. Rearing lambs resulted in lowered wool production and this penalty apparently increased with succeeding parities particularly for ewes rearing twins. Despite the

Table 6.16. Effect of reproductive level on fleece weight (kg)

Reproductive level	Fleece weight at parity:-				
	1	2	3	4	5
Barren ewes	1.81	1.74	1.70	1.68	1.57
Lambed/0 reared	1.51	1.40	1.43	1.37	1.30
Lambed/1 reared	1.66	1.45	1.42	1.38	1.26
Lambed/2 reared	1.66	1.49	1.27	1.23	1.07

Approximate standard error of a difference = 0.05kg apparently large effects, accounting for reproductive level on fleece weight had only small influences on estimates of variance components. Including reproductive level in a genetic model increased the estimates of heritability and repeatability of fleece weight from 0.44 and 0.59 to 0.47 and 0.61 respectively.

(vi) Carry-over effects between parities

The possibility that performance at one age influenced performance in the subsequent year was examined by estimating the effect of reproductive level on body weight at the ensuing mating. Reproductive level at parity (x) was expressed as described in the previous section and fitted as a fixed effect on body weight at parity (x + 1) (Table 6.17). The significant interaction of reproductive level with parity arose largely from smaller effects, on an absolute scale, of first parity reproduction on body weight. When differences were expressed as percentages, there was an average reduction in body weight compared with barren ewes of 4 percent for ewes lambing but rearing no lambs and 12 percent for ewes rearing one lamb to weaning. Although ewes rearing two lambs were given preferential treatment on lowground between the birth and weaning of their progeny, the effect on body weight was very similar to that for ewes rearing a single lamb on the hill. Accounting for this carry-over effect of previous reproductive performance on body weight substantially reduced the within-ewe component of variance for adult body weight resulting in both an increase in heritability (0.29 to 0.31) and repeatability (0.61 to 0.69).

Carry-over effects directly on reproductive performance

Table 6.17. Effect of reproductive level at parity i on body weight at parity (i + 1)

	Body weight (kg) at parity:-			
Reproductive level	2	3	4	5
Barren	42.9	47.6	49.3	48.8
Lambed/0 reared	41.3 (-4%)	45.5 (-4%)	46.9 (-5%)	46.6 (-4%)
Lambed/1 reared	38.7 (-10%)	41.9 (-12%)	43.2 (-12%)	43.0 (-12%)
Lambed/2 reared	37.5	41.4	43.3	43.0

Approximate standard error of a difference = 0.5kg could also be shown to exist but with much less precision (Table 6.18). Ewes barren at one age had a significantly higher litter size at their next parity than at subsequent parities. Conversely, ewes rearing lambs had slightly lower litter sizes at their next parity than at later parities.

These carry-over effects represent negative environmental correlations between parities. They were, perhaps, of most importance in inducing a negative correlation between ewe fertility and litter size in successive parities, mediated through body weight changes.

DISCUSSION

Adequacy of data set

Before considering the implications of the results, the limitations of the design and the methods of analysis should be reviewed. Flock replacements were selected at random so that biasses in sire variance components due to directional selection would be negligible. However, the flock was designed as a control flock to measure selection responses and was not an optimal design for parameter estimation. The average size of half-sib families was too small for efficient estimation of moderate heritabilities for normally distributed traits (Robertson, 1959). In the case of reproductive components, where the distributions were binomial and the expected heritabilities low, the design was shown to be inadequate for parameter estimation. The same inadequacies are apparent in other 'large' data sets that have been used to estimate genetic parameters of reproductive traits in sheep (Young, Turner and Dolling, 1963, McGuirk, 1973, Forrest and Bichard 1974, and

Table 6.18. Effect of reproductive level at parity i on litter size at parity (i + 1) and at subsequent parities.

Reproductive level at parity (i)	Litter size:- Parity (i + 1) (± standard error)	Subsequent parities (± standard error)
Barren	1.172 (±.014)	1.104 (±.014)
Lambed/0 reared	1.124 (±.015)	1.122 (±.014)
Lambed/1 reared	1.079 (±.006)	1.095 (±.006)
Lambed/2 reared	1.359 (±.031)	1.402 (±.038)

Eikje, 1975). Faced with these problems, genetic correlations of unity were assumed between the same trait at different ages so as to estimate a single heritability of each trait pooled across age. McGuirk (1973) and Forrest and Bichard (1974) computed estimates of genetic correlations between ages of ewe and found no significant departure from unity but individual correlations had extremely large sampling variances. It is clear that if we wish to estimate genetic correlations between ages or test for changes in heritability with age for reproductive traits in sheep populations, more suitable designs or larger data sets will be required.

Culling of ewes from the breeding flock on the basis of previous performance represents a possible source of bias in the estimation of genetic parameters. In this case, analysis showed that barren ewes were selectively culled, a similar situation to that reported by McGuirk (1973) and Forrest and Bichard (1974) in their data sets. Estimates of both repeatability and heritability of barrenness are likely to be biassed downwards by such culling so that the incorporation of barrenness as a trait for selection in hill sheep must remain an open question.

Genetic parameters of lifetime traits in sheep

There have been a number of reviews of literature estimates of genetic parameters for lifetime performance traits in sheep collected across breeds. Most reports have highlighted the similarities between estimates assuming, perhaps, that sheep of differing breeds or in different environments have a common genetic basis for the expression of these traits. The estimates obtained here from Scottish Blackface sheep on the hills of Scotland were compared with these other reports.

Land, Atkins and Roberts (1982) reviewed heritability and repeatability estimates for litter size and reported unweighted means of 0.10 and 0.15 respectively. The estimates of Purser (1965), fully supported by the present estimates from the same population of sheep, were the highest values reported in the review. This is surprising since the mean litter size (or incidence of twinning) in the Scottish Blackface sheep was the lowest of all studies reviewed by Land et al. (1982). The provision of preferential nutrition to ewes rearing twins would not explain the apparent higher repeatability since this group of ewes were subsequently no heavier (Table 6.16) nor more prolific (Purser, 1965) than ewes kept on the hill. The genetic correlation between litter size and ewe body weight of 0.66 was considerably larger than that reported in other studies (Land et al., 1982) or those observed as realised correlated responses to selection on litter size by Clarke (1972) and Hanrahan (1979). Estimates of the additive genetic variance in litter size and the genetic covariance between litter size and body weight would suggest differences between hill sheep and other breeds. However, it is impossible to determine whether such differences were true breed differences or some consequence of the environment and management of hill sheep. It is of interest that unusually large responses of ovulation rate to body weight changes induced by nutritional level have been reported among Scottish Blackface sheep as distinct from other breeds (Morley, et. al. 1978).

The presence of carry-over effects between ages, or negative environmental correlations, have also been suggested in the data of Eikje (1975) for litter size and Shelton and Menzies (1970) for fertility. Given the relative harshness of the hill environment, it is reasonable that these negative correlations may be more important in Blackface sheep than in other breeds. Such correlations would tend to lower expected rates of response to selection.

Literature estimates of the heritability of lamb survival as a trait of the lamb (direct genetic effects) have varied widely from zero (Piper and Bindon (1977)) to 0.16 (Shelton and Menzies, 1970). Hanrahan (personal communication) found evidence of maternal genetic effects among Merino ewes for lamb survival, indicating a heritability of about 0.1 from a similar data set to that used by Piper and Bindon (1977). Cue (1981) examined lamb survival as a trait of the lamb in this Blackface population and found some evidence of additive genetic variation, with apparently more amongst twin lambs than singles. Here, where lamb survival was treated as a trait of the ewe, there was little evidence of any further genetic variance for lamb survival as a maternal trait above that apparent amongst lambs as a direct trait.

There are few comparable estimates of genetic parameters for body weights in sheep extending from birth to maturity. Martin et al. (1980) reviewed literature estimates of the heritability of weights from birth to about four months of age and genetic correlations between them. They concluded that there was considerable variation in the heritability of weaning weight from about zero to 0.5 and that the genetic correlations between weights from birth to weaning were very high, consistently in the range of 0.5 to 1.0. Baker et al. (1979) reported the heritabilities of weights from 4 to 18 months of age amonst New Zealand Romney ewes and rams, and genetic correlations between these weights. They showed weaning weight to have a significantly lower heritability than later weights but that the genetic correlations between all weights were very high (0.7 to 1.0) and similar to those reported by Ch'ang and Rae (1972) in the same breed. The important features of the estimates obtained in this study were the low heritabilities of preweaning weights and the somewhat low genetic correlations between weights at birth, up to weaning and at maturity. These results could be regarded as a consequence of the importance of maternal environment and genotype on a lamb's weight prior to weaning. The lambs own genotype had little effect on its body weight up to weaning and was only expressed subsequently, albeit in the presence of substantial carry-over effects of maternal influence.

The heritability of fleece weight in Blackface sheep was about 0.5 which was in good agreement with estimates from a range of breeds reviewed by Cunningham and Gjedrem (1970). The genetic correlations between fleece weight and body weight and between fleece weight and litter size were close to zero, which was the average of all estimates of these correlations reported in the literature (Cunningham and Gjedrem, 1970 and Land et al. 1982). Not surprisingly though, individual estimates show wide variation about these average values and caution must be exercised in using such averages widely.

Implications for hill sheep improvement

The economic return from hill sheep can be regarded as a function of reproduction survival and maintenance of the breeding female and lamb growth. The number of progeny surviving to marketable age is clearly the relevant measure of ewe reproduction but we have seen that lamb survival has a very low effective heritability. Although estimates of the heritability of barrenness were biassed downwards by culling, it would seem advisable to base selection for increased reproduction rate on litter size at birth. There are a number of possible methods of achieving response in litter size and here we will consider some simplified examples:-

(i) Direct selection based solely on dam's litter size. With a flock structure of five age groups, each ewe could have, on average, three records of litter size at the time of selection of her progeny at 18 months of age.

(ii) Indirect selection based on adult body weight of individuals. Here we assume that selection is for 18 month body weight of males and females and that the estimated heritability of ewe body weight and genetic correlation between body weight and litter size are appropriate parameters.

(iii) Index selection combining dam's litter size records and 18 months body weight.

(iv) Restricted index selection using dam's litter size records but effecting no genetic change in 18 month body weight.

The expected responses to one generation of selection per unit standardised selection differential applied are shown in Table 6.19 for the alternative selection methods. The expected increase in number of lambs weaned will be less than that for litter size because of the incidence of barren ewes and mortality of lambs, particularly differential mortality between single and twin born lambs.

The results of Table 6.19 are very sensitive to the true value of the genetic correlation between body weight and litter size. Thus, it is critical that the conclusions assume that the estimate used as an appropriate population value.

Firstly, indirect selection on body weight alone would result in 40 percent greater response in litter size than selection directly on dam's litter size record. The proportional change in body weight would be of the same magnitude as the proportional change in litter size. This comparison of direct and indirect selection responses in litter size is only applicable to 18 month body weight. If selection was based on body weights at younger ages the advantage of indirect selection would rapidly decline. The estimated genetic correlations between lifetime litter size and body weights of hoggets, and lambs post- and pre-weaning were 0.59, 0.37 and 0.17 (all ± 0.2) respectively. This decline in the genetic correlation coupled with declining heritabilities of body weight (Table 6.11), leads to expected correlated responses in litter size to selection on body weight equivalent to direct selection in the case of hogget weight but substantially lower than direct selection for pre- and post-weaning weights. Similarly, the additional response from index selection above direct selection

Table 6.19. Expected responses in litter size and body weight to one generation of selection per unit standardised selection differential.

Selection trait	Response to selection (% of mean) in:-	
	Litter size	Body weight (kg)
Dam's litter size	0.026 (2.4%)	0.58 (1.5%)
Body weight	0.037 (3.4%)	1.33 (3.3%)
Index combining dam's litter size and body weight	0.040 (3.6%)	1.30 (3.3%)
Index selection on dam's litter size with complete restriction of body weight change	0.011 (1.0%)	0

Assumed parameters

Heritabilities : Litter size 0.12
Body weight 0.29

Correlations : Genetic 0.66
Phenotyopic 0.20

declines from 50 percent for adult body weight to 30 percent, 10 percent and zero for hogget, post-weaning and pre-weaning body weights respectively. In this situation, the selection and use of rams as sires at 7 months of age may not be of any advantage in terms of genetic response. The opportunity for indirect selection is much less and there will be less than an average of three records available on all dams. Thus, the decrease in generation interval from using young sires may be more than offset by the decline in accuracy of selection on litter size.

Secondly, effective genetic improvement of litter size will result in correlated responses in adult body weight since complete restriction of body weight change substantially lowers expected responses in litter size (Table 6.19). Such body weight increases may, in part, be beneficial in increasing early growth rate of surplus lambs, but they will also impose a cost in terms of increased feed requirements for maintenance and production of a larger, more prolific breeding ewe. It is difficult to assess the economic impact of increased feed requirements within an extensive grazing enterprise. For example, it is unclear whether these requirements should be treated as the cost of providing additional supplementation at critical periods of the year or whether total feed should be regarded as a fixed resource and stocking intensity of the enterprise reduced as the requirements of each animal increase. Regardless of the methodology used, the expected responses in body weight are sufficiently high such than any selection objective for improvement of hill sheep should include a negative economic weight for ewe body size *per se*.

Thirdly, the estimated parameters and expected responses to selection have been based on a management system routinely providing preferential nutrition to ewes rearing twin lambs. The consequences of not providing such additional attention are not estimable but may result in lowered expected response in litter size due to more negative environmental correlations between parities and, perhaps, lower estimates of heritability and repeatability.

The choice of appropriate selection criteria to improve lamb growth involves similar considerations to those noted for ewe reproduction. In terms of direct genetic effects it would be clearly more efficient to base selection on a post-weaning body weight because of higher heritability than and high genetic correlation with weight at weaning. However, increasing age at selection will lead to increased correlated responses in adult body weight and so increased maintenance requirements. For preweaning body weights a heritability of less than 0.1 for maternal genetic effects was indicated (Chapter 4), so that slow response is possible for maternal ability. Again, multiple records for a ewe would be available at the time of selection of her progeny but the increase in accuracy from such additional records is relatively small since the trait is moderately repeatable.

CHAPTER 7

SELECTION FOR AN INDEX OF CANNON BONE LENGTH WITH RESTRICTION ON BODY WEIGHT : CORRELATED RESPONSES IN THE COMPONENTS OF LIFETIME PRODUCTIVITY

INTRODUCTION

In this Chapter we consider the realised correlated responses to selection in lifetime production characteristics. The traits examined included body growth from birth to maturity, reproductive performance and its components, wool production and ewe survival. Additionally, cannon bone length at a later stage of maturity was examined.

Rates of genetic response expressed as regressions on selection differential applied to the character under selection were estimated initially. By using information reported in previous chapters on realised heritability of the selected character and estimated heritabilities of the correlated characters in an unselected population, estimates of realised genetic correlations were derived. These realised correlations in the selected lines were then compared, in both magnitude and precision, with base population genetic correlations estimated from the unselected lines.

MATERIAL AND METHODS

(i) Sheep and management

All aspects of the environment, the management of the animals and selection procedures employed have been described in Chapter 3.

(ii) Measurements and records

The measurement of body weight, fleece weights, reproductive components and ewe survival were defined in Chapter 6. Cannon bone length was measured on ewes at 14 months of age (CBL14).

For realised correlated responses to selection, data were available for all lambs born between 1956 and 1974 inclusive in the

CONTROL, LONG and SHORT lines. Body weights at birth (W0) and 2 months of age (W2) were recorded on all lambs of both sexes; weaning weight (W4) on all female lambs; all other measurements were recorded only on those ewes selected to enter their respective breeding lines at 18 months of age and survived to the time of measurement.

The data set used to estimate base population genetic correlations between the selection criterion (COR) and the various lifetime traits was the random-bred CONTROL line (lambs born 1956-74) and the BASE flock (1954-55).

Approximate numbers of records available in the CONTROL and BASE flocks were shown previously in Chapter 6. Similar numbers of records were available in each of the LONG and SHORT flocks in each year as there were in the CONTROL flock.

Some additional information was also obtained on adult ewe productivity from the LONG, SHORT and CONTROL flocks in another environment. Ewes born between 1967 and 1971 were transferred from Stanhope at 6 years of age to lamb in a less harsh upland environment at 7 years of age.

(iii) Statistical analysis

Realised correlated responses - single record traits

Individual records for each trait in each line were first adjusted for any significant effects of hirsel, winter treatment, ewe age, birth type and birth date as estimated previously from the BASE and CONTROL flock data set (Chapter 6). The means for each character in each year of the experiment were then calculated separately for each line. However, apart from pre-weaning records, these means were from a selected sample of all ewes born in each selection line. The phenotypic selection differentials for COR that were applied amongst ewes each year in each line are shown in Table 7.1. There was no relationship between phenotype for COR and survival so that these selection differentials were appropriate for measurements at all ages after weaning. In order to account for the response due to current generation selection, the year means for each line were adjusted using the estimated phenotypic regression of each character on COR and the selection differential for COR.

Realised correlated regressions were estimated for continuously distributed traits (body weights, fleece weight and CBL14) by computing the regression, through the origin, of cumulative correlated responses (adjusted for current generation response) on the cumulative selection differentials for COR. An appropriate variance-covariance matrix for each of the correlated responses was derived as described in Chapter 5 and used to generate a generalised least-squares solution for the realised correlated regression coefficient and its standard error. The one difference in the formulation from Chapter 5 concerned the estimate of measurement error. Previously we had predicted the variances of the difference between two lines for drift involving N (number of individuals selected as parents) and M (number of individuals measured) and for measurement error of the form $2\sigma^2(1-k)/M$. With the correlated traits measured at times other than the time of selection, the M in measurement error was replaced by K, the number of individuals measured for the particular trait, where M>K for traits measured after two months of age. Initially, symmetry of

Table 7.1. Average selection differentials for COR applied amongst ewes in each line in each year.

Year of birth	Selection differential (cms) in:-	
	LONG	SHORT
1956	+0.11	-0.06
1957	+0.02	-0.06
1958	+0.02	0.0
1959	+0.10	-0.11
1960	+0.10	-0.12
1961	+0.16	-0.10
1962	+0.11	-0.06
1963	+0.05	+0.02
1964	+0.05	-0.04
1965	+0.11	-0.06
1966	+0.07	-0.01
1967	+0.05	-0.02
1968	+0.05	+0.01
1969	+0.09	+0.07
1970	+0.05	-0.01
1971	+0.03	-0.05
1972	+0.11	-0.10

response was tested by estimating the correlated regression for the LONG line as a deviation from the CONTROL and similarly for the SHORT line. In the absence of asymmetry, the regression was based on divergence between the LONG and SHORT lines.

For binomially distributed traits (reproductive components and ewe survival) variation between years and parities affect both the means and variances of the observed responses. In order to remove possible scale effects on the estimates, realised correlated regressions were computed from binomial proportions using a probit transformation within the program GLIM (Baker and Nelder, 1978). These regressions were, then, weighted by both the number of observations and the mean. The probit link function was used principally because the variance of the transformed scale is unity while the properties of the alternative, logistic transformation, are perhaps less well known. Analyses were performed for each trait at each parity and then combined across parities, testing for similarity of response on the transformed scale. The variances of these regression estimates were biassed downwards since they included no terms for genetic drift. From Chapter 6, the only trait with a reasonable estimate of heritability, both in terms of magnitude and precision, was litter size. A generalised least-squares regression estimate of correlated response on selection differential for litter size was therefore attempted with the assistance of R. Thompson.

From an analysis of binomial proportions using the probit link function, the linear predictors of litter size were obtained:-

$$T_{ij} = R_j + b\ S_{ij}$$

where T = linear predicted value for each line)i = 1, 2 for LONG and SHORT) in each year (j = 1, $\leqslant$ 16).

R = 'year' effect common to both lines

S = observed selection differentials for COR

b = regression coefficient of litter size (probits) on selection differential

These linear predictors correspond to thresholds on a unit normal curve. For observed litter size in one year for the LONG and SHORT lines, the response to selection on this underlying scale will be:-

$$T_1 - T_2 = b(S_1-S_2)$$

On the observed (1,2) scale, this response will be the area under the normal curve lying between the two thresholds, viz:-

$$P = \frac{1}{\sqrt{(2\pi)}} \int_{T_2}^{T_1} e^{-x^2/2} \, dx$$

A normal approximation for this response (P) would be to find the height of the ordinate of the curve (Z) at the midpoint of T_1 and T_2 so that:-

$$P \approx Zb(S_1-S_2)$$

Thus responses on the observed scale are determined by the selection differential applied (S), the regression on the underlying scale (b) and a scaling factor Z which is in turn dependent on S, b and the average year effect, R.

The approach can be extended to observations at a number of years by including a deviation from the fitted regression.

Response in litter size at year (i) $= \Sigma i(S_{1i}-S_{2i})\ b + (P_i - E_i)$

where P = observed litter size difference expressed as ewes with twins as a proportion of all ewes lambing

E = expected litter size difference estimated as the difference between the normal probability integrals of T_{1i} and T_{2i}.

In regression terms, then, we have a working x variate of scaled selection differentials, ΣS (where S = divergent selection differentials) and a working y variate of $\Sigma Sb + (y-\mu)$, where $(y-\mu)$ is an observed-expected deviation.

The variance-covariance matrix of responses appropriate to the Y variate was built up separately for expected measurement error variance and expected genetic drift variance using a similar procedure to that described in Chapter 5. Drift variances and covariances were estimated on an assumed underlying normal scale with a variance of unity and a heritability for litter size of 0.37 for all parities (estimated from $h^2p(1-p)/z^2$ as suggested by Robertson and Lerner (1949) where h^2 is the heritability of litter size on the observed 1,2 scale across parities, p is the average incidence of twinning and z the height of the normal curve corresponding to p). The drift variance-covariance matrix (D) was then scaled back to the observed scale using the appropriate vector of Z described previously (Z'DZ). Terms for measurement error were then added to the diagonal elements of the scaled drift matrices using Q(1-Q) as the variance of litter size on the observed scale where Q = incidence of twins in each line in each year. The variance-covariance matrix (V) of the weighted divergences between the LONG and SHORT lines consisted of the scaled variance-covariance matrix and measurement error variance in both the LONG and SHORT lines. The appropriate generalised least-squares equation for b was then solved using an initial value of b and the procedure was iterated using the new estimate of b until convergence.

Regressions of correlated response on selection differential have the following expectation:-

$$b_c = r_G \ h_1 h_2 \sigma_2 / \sigma_1$$

where b_c = realised correlated regression

r_G = realised genetic correlation

h_1^2 = realised heritability of direct trait

h_2^2 = realised heritability of correlated trait

σ_1 = phenotypic standard deviation of direct trait

σ_2 = phenotypic standard deviation of correlated trait

Of these parameters, the realised genetic correlation and the realised heritability of the correlated trait are unknown. Estimates of the heritability of the correlated traits in the base population have been presented previously (Chapter 6), but we would expect realised heritability to be lower than this estimate due to the operation of some within-family selection and the generation of linkage disequilibrium. It was argued in Chapter 5, for the character under selection, that the net effect of these two factors resulted in a realised heritability that was 15 percent lower than the base population estimate. A similar derivation for the realised heritability of correlated traits was used to estimate the variance-covariance matrices of responses and for estimating realised genetic correlations. The variance of the realised genetic correlation was derived from expansion of the previous expression as:-

$$V(r_G) = \frac{V(b_c)}{h_1^2 h_2^2} + \frac{V(h_1^2)}{4(h_1^2)^3 h_2^2} + \frac{V(h_2^2) b_c^2}{4h_1^2 (h_2^2)^3}$$

Certain covariance terms have been ignored which would tend to reduce $V(r_G)$ but the phenotypic variances of the two traits were assumed to be known without error which could increase the variance. Therefore, the variance of the correlation should be regarded as only approximate.

Realised correlated responses - multiple record traits

In Chapter 6 it was concluded that the estimated genetic correlations between parities for body weight, for fleece weight and for litter size were effectively all unity. Provided that the correlated responses in each of these traits showed no significant differences across parities, the individual parity responses could be combined to obtain a single estimate of the realised genetic response. The observed responses for, say, body weight at each parity were first scaled by the phenotypic standard deviation appropriate to weight at that parity. Drift and measurement error variances and covariances appropriate to these standardised responses at each parity in each year were estimated as before. In addition, terms were added to the 'block' diagonals for the phenotypic covariance between means for weights recorded on the same animals at different parities. These terms were of the general form:-

$$\frac{L.\text{cov}(X_1, X_2)}{M.N}$$

where $\text{cov}(X_1, X_2)$ is the phenotypic covariance between the two traits X_1 and X_2 and where M and N animals respectively are measured for the traits, and L of these animals have measurements on both traits.

Where weights were recorded on all animals surviving ($L=N$) and the responses were standardised, these covariance terms reduced simply to r/M where r is the phenotypic correlation between weights X_1 and X_2 and $M>N$.

Base population genetic parameters

The genetic correlations between COR and all components of lifetime productivity were estimated by paternal half-sib components of variance. All animals from BASE and CONTROL lines with records available on a particular pair of traits were included in the analysis. The individual records had been previously adjusted for the important fixed effects, excluding year of birth, appropriate to that trait as estimated for COR (Chapter 4) and lifetime traits (Chapter 6). Standard errors of the genetic correlations were estimated as functions of the variance and covariance components

(Becker, 1975).

For body weights, fleece weights and litter size recorded at ages 2 to 6 years (parities 1 to 5) an analysis combined across parities to estimate a single genetic correlation for each trait was also undertaken. The mean performance of a ewe for a particular trait was estimated, adjusting for the average effect of parity. A weighting factor for each individual ewe was then calculated from:-

$\frac{m}{1 + (m-1)t}$ where m = number of records available
t = repeatability of trait

Between- and within-sire (co) variance components were estimated from both weighted and unweighted analyses of variance. If the data were balanced with respect to number of records, the expectations of the between-sire (co) variance components would be equal in both the weighted and unweighted analysis whereas the within-sire components would alter. Both analyses were computed and the genetic correlation estimated as:-

$$r_{G(xy)} = Cov_A(x,y) / (V_A(x)\ V_A(y))^{1/2}$$

where V_A = between-sire variance component for x (COR) or y (correlated lifetime trait)
Cov_A = between sire covariance component between x and y

RESULTS

(i) Cannon bone length at 14 months of age (CBL14)

Between 2 and 14 months of age, average cannon bone length in the CONTROL line increased by slightly more than 2 cms or about 24 percent of its length at 2 months of age (Table 7.2). Total phenotypic variances for CBL14 and CBL2 were similar although for

Table 7.2. Phenotypic and genetic parameters of CBL14 estimated in the CONTROL AND BASE flock.

	COR	CBL2	CBL14
Mean (cm)	10.28	10.04	12.43
Phenotypic variance (cm^2)	0.150	0.295	0.309
Heritabilities phenotypic and genetic correlations * (± standard error)			
- COR	0.53±.05	0.67	0.61
- CBL2	0.91±.03	0.33±.05	0.65
- CBL14	0.82±.07	0.77±.09	0.49±.09

*Heritabilities (on diagonal), phenotypic correlations (above diagonal) and genetic correlations (below diagonal) estimated from paternal half-sib analyses of variance.

CBL14 the genetic component was greater and the environmental component smaller than the corresponding estimates for CBL2.

The phenotypic regression of CBL14 on COR was estimated separately within the CONTROL, LONG and SHORT lines. The estimated within generation regressions were 0.90, 0.88 and 0.88 cm per cm respectively indicating no significant effect of selection on this regression. The observed responses in the selected lines were then adjusted for the current generation selection differentials (Table 7.1) by using the estimated regression from the CONTROL line.

Realised correlated regressions for the LONG and SHORT lines, estimated separately as deviations from the common CONTROL, were 0.59±0.07 and 0.66±0.06 cm response in CBL14 per cm selection differential in COR respectively. The asymmetry in response was not significant although, predictably, it was in the same direction as that observed in CBL2 (Chapter 5). Correlated responses were therefore based on the divergences between the LONG and SHORT lines. The estimated regression was 0.643±0.033. The equivalent realised genetic correlation was 0.98±0.11, which was not significantly higher than the base population estimate (Table 7.2).

(ii) Body weights from birth to maturity

Responses in the selected lines for all recorded body weights showed no evidence of any asymmetry of response. The reported results, then, were restricted to estimate of divergence between the LONG and SHORT lines. The phenotypic regressions used for adjusting observed responses in the various weights recorded after weaning are given in Table 7.3. Predicted correlated responses in body weight at each age, equivalent to 4 cm of

Table 7.3. Correlated responses in body weights from birth to maturity.

Body weight at various ages (months)	Phenotypic regression of W on CORCBL (kg cm^{-1})	Control line Mean(kg)	Divergence at 5 cm selection differential:-		Genetic correlations (± standard error)	
			kg(±se)	σ^+	Realised	Base population
W0	-	2.9	0.36±.07	0.66	0.28±.07	0.45±.13
W2	-	12.1	0.54±.25	0.24	0.11±.06	0.18±.16
W4	-	21.2	1.16±.30	0.36	0.24±.12	0.00±.22
W6	1.41	25.1	1.40±.59	0.48	0.15±.06	-0.15±.18
W12	1.28	20.7	1.44±.48	0.57	0.19±.07	-0.05±.21
W14	2.62	28.5	1.67±.50	0.56	0.21±.08	0.05±.23
W16	3.97	33.9	2.18±.74	0.64	0.18±.07	0.19±.20
W18	3.88	37.0	2.06±.82	0.59	0.16±.07	0.26±.19
W30	5.23	40.0	2.49±1.03	0.56	0.16±.07	0.30±.20
W42	5.07	42.5	2.90±1.12	0.64	0.18±.08	0.15±.25
W54	5.09	43.3	2.56±1.33	0.54	0.14±.08	0.17±.25
W66	2.32	44.0	2.90±1.45	0.62	0.16±.09	-0.10±.29
Adult weights (W18 - W66)				0.61	0.17±.06	0.21±.17

$+\sigma$ divergence expressed in phenotypic standard deviation units of the particular body weight divergent selection differential (corresponding to the year 1970 or year 15 of the experiment), showed increasing divergence between the LONG and SHORT lines with increasing age (Table 7.3). Since the mean and variance of body weight also increased with age it seemed appropriate to scale the predicted divergences by the phenotypic standard deviation of weight at each age as estimated in Chapter 6. These phenotypically scaled responses (Table 7.3) still showed a differential age response with relatively small response in preweaning weights (W2, W4), larger responses up to first mating (W6-W16) and even greater responses among adults (W18-W66). This, of course, was precisely the pattern of change in heritability with age described in Chapter 6, so that estimates of 'realised' genetic correlations, with the possible exception of birth weight, showed no evidence of age trend (Table 7.3). Base population genetic correlation estimates were much less precise but were generally of a similar magnitude (Table 7.3).

In Chapter 6 it was argued that adult weights could be grouped together since the genetic correlation between them was effectively unity. The same principle was applied here for the realised correlated responses using the multiple records model described in the Methods. The sampling variance of the predicted divergence for grouped weights was only marginally smaller than that of a single weight (Table 7.3). This result merely reflects the domination of genetic drift over measurement error in the variance of the correlated response. For example, for W18 the proportional contributions of drift and measurement error to the sampling error of the regression were 0.73 and 0.27 respectively. With the repeated records model involving the five adult weights, the absolute contribution of drift would remain about the same while the measurement error would be reduced to approximately [1/(1+(k-1)t] of its single record value, where k is the number of repeated records and t the average repeatability. The actual reduction in variance observed was very close to this prediction. The end result is that repeated records of the same trait contribute little improvement in the precision of estimates of correlated response in experiments of a reasonable duration.

(iii) Fleece weights

Realised responses in fleece weights recorded at annual intervals showed a slight, but not significant, positive response in fleece weight at one year of age but virtually zero response at later ages (Table 7.4). There was no asymmetry between the LONG and SHORT lines. The negative genetic correlations estimated from the unselected lines were not confirmed by the realised responses to selection (Table 7.4).

(iv) Reproductive performance

Net reproduction rate was defined as the number of lambs weaned per ewe mated and the differences between the lines were estimated from a model that included year, parity and the covariate, selection differential (Table 7.5). There were apparent differences between parity in the divergence of the selected lines with increasing rate of response with increasing age. However, the distribution of this trait and its heritability are not obvious and so no terms for genetic drift were included in the standard errors of the divergences.

Table 7.4. Genetic correlations between adjusted cannon-bone length (COR) and fleece weight at annual intervals.

Fleece weight at age :-	Genetic correlation (± standard error):-	
	Realised estimate	Base population estimate
1 year	0.08±.06	-0.10±.15
2 years	0.02±.06	-0.09±.16
3 years	-0.03±.06	-0.15±.19
4 years	-0.01±.06	-0.44±.22
5 years	0.02±.07	-0.40±.23
6 years	0.01±.07	-0.19±.22

Table 7.5. Lambs weaned per ewe mated at each parity for the CONTROL line, and for the LONG and SHORT lines estimated at 4 cm divergent selection differential for COR.

Age of ewe	Lambs weaned per ewe mated:-			Divergence (± standard error) LONG-SHORT
	CONTROL	LONG	SHORT	
2 years	0.558	0.591	0.580	0.011±.025
3 years	0.738	0.826	0.710	0.116±.030
4 years	0.831	0.890	0.778	0.111±.050
5 years	0.805	0.930	0.761	0.169±.028
6 years	0.748	0.902	0.720	0.187±.078

From Chapter 6, estimates of genetic parameters for the components of reproductive performance among unselected animals showed that only litter size had levels of genetic variability high enough for realistic estimation of heritability. Litter size responses were examined using the variance-covariance matrix of responses incorporating both genetic drift and measurement error. The responses in the other reproductive components were analysed using measurement error only for the variance of the observed responses.

Realised genetic correlations for litter size at each parity are shown in Table 7.6 and compared with base population estimates. There were no significant differences between parities and the realised genetic correlation across parities was 0.12. The realised genetic correlations for each parity were consistent in sign and magnitude whereas the estimated base population genetic correlations were much less consistent and considerably less precise. Since the responses were analysed on a transformed scale (probits) the expected response in litter size was dependent on the mean. For a genetic correlation of 0.12, a heritability of litter size of 0.37 (on the underlying scale) and a selection differential of 4 cm divergence between the lines in COR, the expected responses in litter size on the observed scale are shown in Figure 7.1. In addition, the predicted responses from the separate parity regressions are also shown. It can be seen that the scale effects on responses were of little importance with respect to interpretation for the first three parities since untransformed data would have yielded a similar result. However, the responses from later parities and the more favourable upland environment (parity 6)

Table 7.6. Genetic correlations (± standard error) between CORCBL and litter size.

Location and Age of ewe	Genetic correlation (± standard error)	
	Realised	Base population
Hill		
2 years	0.25±.10	-0.03±.34
3 years	0.16±.09	0.12±.26
4 years	0.06±.08	0.37±.35
5 years	0.17±.09	0.29±.31
6 years	0.12±.10	-0.04±.56
Upland		
7 years	0.11±.09	-
All ages		
2-6 years (base)		0.08±.20
2-7 years (realised)	0.12±.07	

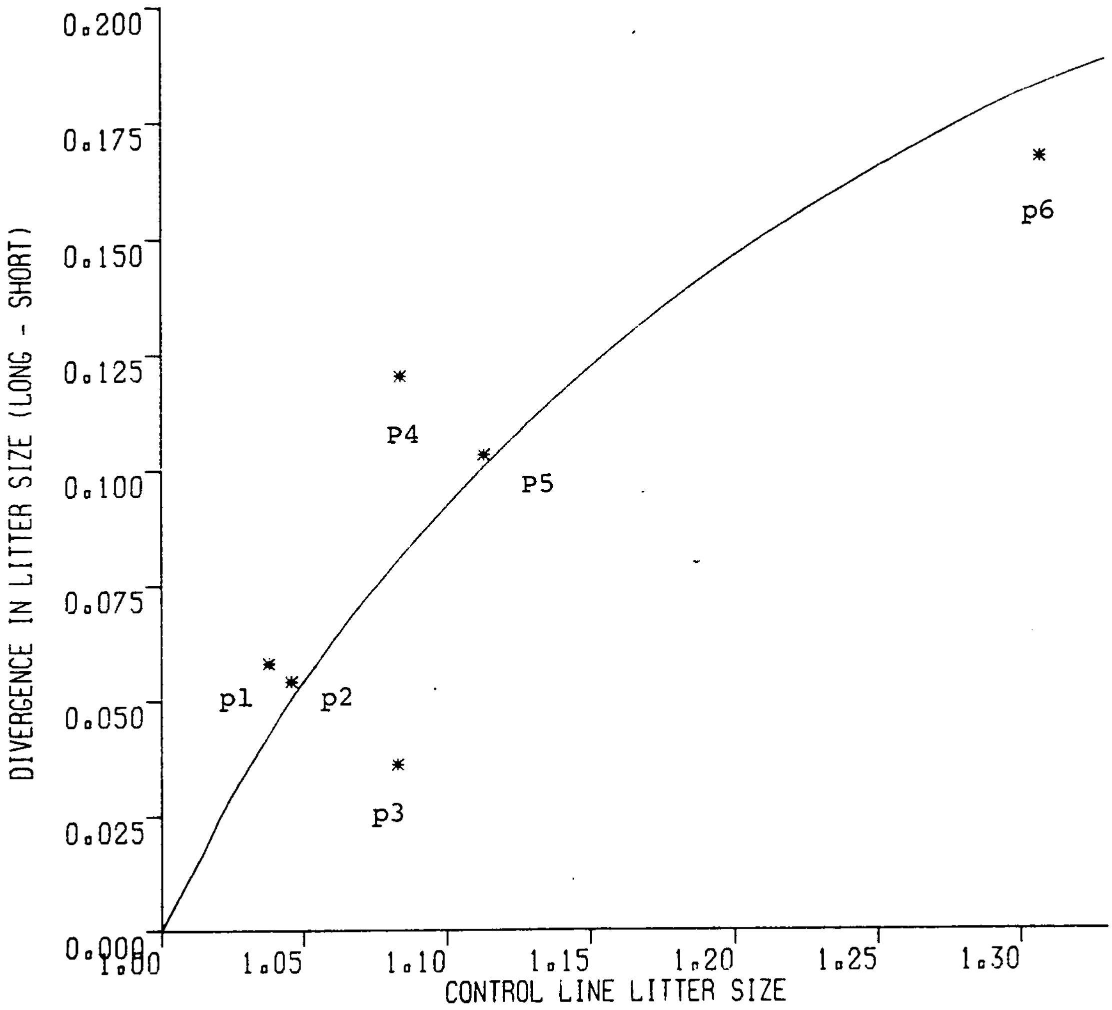

FIGURE 7.1. Expected divergence between LONG and SHORT lines in litter size at 4cm selection differential for COR. The line was the estimated regression across all parities while the predicted points were derived for each parity separately.

would have produced a much higher regression of response in litter size on selection differential if they had not been transformed to a more suitable scale.

Regression estimates of the correlated responses in other reproductive components indicate some evidence of response in the proportion of ewes lambing and lamb survival (Table 7.7). It should be recalled that the variance of these estimates contained no terms for genetic drift or phenotypic covariance between parities and so are probably biassed downwards (Table 7.7). For ewes lambing per ewe mated there were no significant differences in the regression of responses (on probit scale) on selection differentials between lines or between parities. The estimate of response indicated a positive genetic correlation between COR and ewes lambing (Table 7.7). For lamb survival there were no significant differences in the regression of response on selection differential between lines or between litter sizes (singles and twins). However, there were significant differences between parities such that among first parity ewes (2 years of age) there was no significant response but amongst older ewes there was an apparent positive genetic correlation between COR and lamb survival (Table 7.7).

The predicted means for the LONG and SHORT lines for each reproductive component on the observed scale after 4cm of divergent selection differential (Table 7.8) show the contribution of the various components to the observed divergence in net reproductive rate (Table 7.8). The dominant components contributing to the divergence were litter size and ewes lambing although their relative

Table 7.7. Realised responses in the components of reproductive performance. Correlated regressions were expressed as response on the underlying probit scale per cm selection differential in COR.

Reproductive component	Correlated regression (± standard error)
Ewes lambing (per ewe mated)	0.052±.016
Litter size (lambs born per ewe lambing)	0.118±.062
Lamb survival to weaning (per lamb born)	
- first parity (2 year old ewes)	-0.019±.027
- later parities (3-6 years)	0.069±.024

* The standard error for litter size was the only component that contained predicted drift variance.

Table 7.8. Predicted line means on observed scale for reproductive components among first and later parity ewes after 4cm of divergent selection differential on COR.

	Predicted line means for:-			
Reproductive component	Parity 1 ewes		Parity 2-5 ewes	
	LONG	SHORT	LONG	SHORT
Ewes lambing (A)	0.83	0.77	0.91	0.87
Litter size (B)	1.06	1.02	1.12	1.05
Lamb survival				
- singles	0.72	0.75	0.92	0.87
- twins	0.44	0.47	0.75	0.65
- all lambs (C)	0.69	0.74	0.88	0.84
Lambs weaned per ewe mated				
- predicted (A,B,C)	0.60	0.58	0.89	0.77
- observed (Table 7.5)	0.59	0.58	0.89	0.74

influences differed in first and later parities. A higher proportion of the lambs born in the LONG line were twins and, although the survival rate of lambs was higher in this line compared with the SHORT, twin survival was still lower than the survival rate of singles. Thus, the estimated difference between the lines in survival of all lambs (lambs weaned per lamb born) was very small at all parities. The parity differences in net reproduction rate observed in Table 7.5 arose from both differential responses in lamb survival between parities and scale effects on litter size. As the mean litter size increased with age up to fourth parity, so did the responses in litter size on the observed scale (Figure 7.1), even though the responses were similar on the underlying scale.

(v) Ewe survival

The proportions of ewes culled at each age from the CONTROL, LONG and SHORT lines were analysed by the same method used for the binomially distributed reproductive traits. There was no evidence of asymmetry of response or significant differences between parities in the regression of the transformed response on selection differential. The overall regression per cm of selection differential for COR was 0.065±.020. Again, the estimates of the standard error contained no terms for expected genetic drift since the estimates of genetic variance for ewe survival were both variable and imprecise (see Chapter 6). The predicted means for the proportion of ewes culled after 4 cms of divergent selection on COR show the higher levels of culling amongst ewes from the LONG line with the CONTROL line intermediate at all ages (Table 7.9).

Table 7.9. Annual disposal of ewes (as a proportion of ewes present) for the CONTROL line, and for the LONG and SHORT lines estimated at 4cm divergent selection differential for COR.

Annual Interval	Ewes culled (or died) at year (i+1) per ewe present at year (i):-		
	CONTROL	LONG	SHORT
2-3 years	0.070	0.076	0.046
3-4 years	0.074	0.099	0.061
4-5 years	0.107	0.119	0.075
5-6 years	0.240	0.286	0.205

DISCUSSION

Selection for increased cannon bone length at 8 weeks of age, adjusted for body weight at the same age, resulted in the following correlated genetic response:-

- increased cannon bone length at a later age
- increased body weights at all stages of growth from birth to maturity
- increased reproduction rate arising principally from increased litter size but with smaller increases in the proportion of ewes lambing and the survival rate of lambs
- increased losses of adult ewes arising from deaths and necessary culling

These results are of interest in terms of their application to sheep improvement generally and Scottish Blackface sheep in particular. In addition, the correspondence between observed correlated responses and those expected from base population genetic parameters would give some measure of the usefulness of selection experiments in deriving correlated responses.

The length of the cannon bone in sheep is a very early maturing body part. In a comparison of five breeds at pasture, Wiener (1967) showed that the final length of this bone was achieved by 12 months of age so that the length recorded in this experiment at 14 months of age can be assumed to be its mature size. At the time of selection, then, the cannon bone had already reached more than 80 percent of its mature size so that selection was applied very late in its development. Thus, it was not surprising that the correlated responses at maturity were of the same relative magnitude as those at the time of selection (both 21 percent of the CONTROL mean at the end of the experiment).

The genetic correlation between the selection criterion and body weight was the same magnitude throughout the animal's life. It was shown in Chapter 6 that the genetic correlations between body weights at different ages were not very high but at least part of the genetic covariance between weights at different ages was apparently due to this consistent relationship between bone length and weight. It should also be recalled that the original aim of the experiment was to alter cannon bone length while restricting body weight change and so the adjustment for the phenotypic regression was included in the index of selection. The fact that correlated responses in body weight were still achieved indicated a disparity between the phenotypic and genetic regressions of CBL2 on WT2. If selection had been based solely on CBL2 the correlated response in body weights at all ages may have been higher. Base population parameter estimates indicated slightly higher genetic correlations between CBL2 and body weight than between COR and body weight but the differences were not significant for any weight.

The correlated response in litter size to selection on cannon bone length was reported previously by Purser (1982) who suggested that the greater response in the LONG line in the upland environment was indicative of a genotype x environment interaction. However, since litter size of Blackface sheep in this experiment was a binomial trait (twins or singles) the apparent genotype x environment interaction could be more simply explained as a scale effect. The more favourable environment allowed a higher phenotypic expression of the trait which would lead to a higher heritability on the observed (binomial) scale but a similar genetic correlation. This genetic association between litter size and bone length need not be causal but may have been mediated through their separate associations with body weight. The realised genetic correlations between adjusted cannon bone length and litter size, and bone length and body weight were 0.12 and 0.17 respectively while the base population genetic correlation between body weight and litter size was 0.66 (Chapter 6). The 'partial' genetic correlation between litter size and cannon bone length, independent of body weight differences, would be only 0.01. The small responses in lamb survival might have a similar basis. Cue (1983) reported overall lamb survival in the LONG and SHORT lines showing no significant response, as also shown here (Table 7.8). Previously, Cue (1981) had examined single and twin lamb survival separately and shown similar positive estimates to those reported here. Importantly, though, the estimates of response were considerably smaller when birth weight was included as a covariate in his model. Thus, the small response in lamb survival was probably a consequence of the correlated response in birth weight, except in first parity ewes.

The difference between the lines in adult ewe survival appeared to have a genetic basis. Several analytical models which included alternative measures of previous reproductive performance produced no adequate explanation of the difference as a result of increased reproductive activity and thus metabolic stress. The response in ewe survival coupled with the evidence of a non-zero heritability of the trait (Chapter 6) would suggest that continuing ability to produce in their environment should form part of an overall selection objective for hill sheep.

In Chapter 5 it was shown that the observed responses to selection in the index under selection and its component traits were of the same magnitude as, but of greater precision than, the predicted responses based on estimated heritabilities and genetic correlations. The genetic correlations between cannon bone length and the measures of body weight and reproductive performance were relatively low. Estimates from the base population were extremely variable and imprecise and, although the estimates were distributed about the realised correlations, would be of doubtful value alone as a basis for predicting correlated responses to selection. Similarly, the scale effects on litter size were an obvious retrospective interpretation of the observed pattern of response. Without observing the actual response to selection and using only base population estimates, the incorporation of scale effects into models of response would be less clear.

On the other hand, the method of analysis employed relied on deriving a variance-covariance matrix for measures of correlated response. This matrix was largely dependent on expected genetic drift principally arising from the expected realised heritability of the correlated trait. These heritabilities were derived from the base population estimates and, in their absence, no estimate of precision of realised responses or comparisons with predicted responses would be possible from an unreplicated selection experiment.

In conclusion, it would be unrealistic to compare realised and predicted responses to selection retrospectively as potentially alternative designs. The realised responses were estimated quite precisely, particularly those involving low genetic correlations. This precision, however, was largely a function of having estimates of base population heritabilities for correlated traits available from a similar population maintained in the same environment. Base population heritabilities and genetic correlations were so imprecisely measured that any prospective estimates of response would have been largely conjectural.

CHAPTER 8

FINAL DISCUSSION AND CONCLUSIONS

The results of this experiment have implications in three separate areas:-

- statistical analysis of selection experiments
- responses to selection for body conformation
- genetic improvement of productivity of Scottish Blackface sheep in a hill environment

ANALYSIS OF SELECTION EXPERIMENTS

(i) Sampling variances of realised parameters

Unreplicated selection experiments pose particular analytical problems since the experiment does not yield a direct measure of genetic drift. Since drift is the dominant source of variance of observed responses after a relatively short time period of an experiment, ignoring drift, as has been done in some previous analysis, is unacceptable and leads to estimates of realised parameters whose precision is substantially biassed downwards. The approach used in this thesis was to estimate the likely variance of each observed response and the covariances between responses across generations, and then to estimate realised regressions in the presence of this variance-covariance matrix of responses. The questions to be answered retrospectively are how useful was this approach to analysis, how appropriate were the theoretical expectations and what alternatives are available?

The formulae used to generate the variance-covariance matrices were based on the theoretical considerations of Hill (1971; 1972a, b). The only additional formulation was to incorporate the approximations for populations with overlapping generations developed by Johnson (1977).

The expected variance of a response was derived from the sum of drift variance and measurement error variance. The drift variance accumulates across generations while the measurement error does not. The covariance between responses observed in different generations is a function of the drift variance at the earlier generation.

The expression for drift variance was simply a deviation from the regression of breeding value for a trait on selection differential for the selected trait. The following situations were specified:

(i) direct response in a single selected trait.

drift variance in selected trait per generation $= h^2\sigma^2(1-h^2)/N$
$= (G - GP^{-1}G)/N$

where h^2 = heritability; σ^2 = phenotypic variance,

N = effective number of parents chosen on selected trait; G = genetic variance ($h^2\sigma^2$);

P = phenotypic variance (^{2}).

(ii) correlated response from single trait selection where the correlated trait is denoted Y, the selected trait X and r is the genetic correlation between X and Y. Therefore,

drift variance in correlated trait per generation $= h_Y^2\sigma_Y^2(1-h_X^2r^2)/N$

(iii) direct response from simultaneous two-trait selection. The formulation is the same as in (i) except that the scalar G now becomes a 2x2 matrix which contains the genetic variances for the two traits on the diagonal and the genetic covariance between the two trait on the off-diagonal. Similarly P becomes a 2x2 matrix of phenotypic variances and covariances. Some equivalent formulae have been developed by Gunsett, Andriano and Rutledge (1982) using a selection index approach.

It can be seen from the above formulae that the variance-covariance matrix for the observed responses depends on the genetic and phenotypic parameters and the population structure. Since the experiment was complete, information was available on the population structure and precise estimates of phenotypic variances and covariances were possible. Using a generalised least-squares model, a prior value for the relevant genetic parameter was chosen to generate a variance-covariance matrix of responses, a solution obtained and the process iterated until the previous estimate and new estimate converged. For the three situations described above, the relevant genetic parameters were genetic variance in selected trait, genetic covariance between selected and correlated traits, and genetic variance-covariance matrix for the two traits in situations (i), (ii) and (iii) respectively. Initial values for genetic parameters were those obtained from an ordinary least-squares analysis (that is, ignoring drift). The generalised least-square solution was achieved within three iterations which is not surprising since the ordinary least squares estimate has been shown to be quite efficient (Hill, 1972a).

Whether the theoretical formulae of Hill (1971) adequately describe genetic drift in selected populations has not been tested. These formulae are based on a number of crucial assumptions, in particular the assumption that variances and covariances are not altered by the selection process. The expected drift in a selected line is reduced from that expected in an unselected line because of the reduction in variance of breeding value among directionally selected rather than randomly selected parents. However, it was shown by Avery and Hill (1977) that selection induces a variance between replicated lines in the genetic variance so increasing the variance of response particularly in later generations. This led Robertson (1977) to a compromise suggestion of using the expected drift in an unselected line for the expected drift in a selected line on the assumption that these two effects on variance cancel each other. Using such a compromise would increase the standard error of the realised heritability reported in this experiment by slightly less than 20 percent. On the other hand, W.G. Hill (pers. comm.) has suggested that, where they have been examined, estimated variances between replicated selection lines have been somewhat lower than theoretically expected variances. A review of such information would be of assistance in deciding upon a suitable expression for, while these expectations will never be perfect for any situation, it is all we have for unreplicated selection experiments and some account of the effects of drift is certainly preferable to ignoring it (Hill, 1980).

The estimation of drift for correlated responses is a special situation requiring prior knowledge of the genetic variance in the correlated trait. Without such prior knowledge, replication is the only means of obtaining an appropriate error variance for the realised correlated responses. Even then, derived parameters such as the realised genetic correlation would not be possible without an estimate of the genetic variance in the correlated trait. In Chapter 7 it was argued that one of the great aids to analysis and interpretation of the correlated responses in this experiment was that a control population was maintained such that the heritability of correlated traits could be estimated. An appropriate formula for drift in correlated traits and inferring a realised heritability from a base population estimate poses difficulties but some prior information is available.

Other assumptions in estimating drift involved the use of a single effective population size and average contributions of genes from different parental age groups. It was shown in Chapter 4 that values for these variables were remarkably consistent both within and between the selected lines and probably little precision was forfeited by these assumptions. More precise estimates of drift in less fortuitous circumstances might be possible using actual relationships among all animals rather than expected relationships based on average population structure parameters. In this regard, the use of co-ancestry relationships (such as the numerator relationship matrix) would be a better basis for estimating expected drift in a selected line, particularly where overlapping generations are involved.

(ii) Expected responses to selection

Some factors influencing expected responses in selection experiments for the trait under selection were reviewed in Chapter 2. Of these, the effects of method of selection (inbreeding avoidance) and linkage disequilibrium have been discussed in relation to the estimate of realised heritability in Chapter 5.

Overlapping generations influence expected responses due to a non-linear approach to an asymptotic rate of response in the early years of an experiment and by inducing genetic differences between animals within a contemporaneous group arising from the differing ages of their parents. In the presence of such influences it is reasonable to question whether the estimation of realised heritability or realised correlated regressions are suitable analytical procedures.

The form of analysis should be dictated by the aims of the experiment. If the aim is to compare realised responses with expectation from base population parameters, then the use of mixed model methodology is appealing. By specifying the actual relationships among animals in a selected line and using an assumed value for the base population heritability, the responses in predicted breeding values for contemporary groups of individuals can be estimated. J.W. James (pers. comm.) has suggested the testing of observed and expected responses to selection using a minimum Chi-squared test based on the variance-covariance matrix of responses to estimate the base population heritability that most adequately describes the observed responses. This approach has the advantage of including linkage disequilibrium and population structure effects within the model since the relationship matrix is specified. On the other hand, the observed response to selection for a specified selection differential is a direct measure (with certain qualifications of population structure) of the likely response to selection for a particular trait. It is often the aim of selection experiments to determine the likely response to selection rather than the more abstract estimate of base population genetic variance.

For direct application of the results of selection experiments, realised heritabilities, at population equilibrium, for characters of economic importance are useful measures of response.

Perhaps this discussion illustrates the deficiencies, not so much of analytical procedures for observed selection responses, but of the simplified models used for predicted selection responses, particularly in populations with overlapping generations. Expected responses are often simply predicted from:-

$$R = Sh^2$$

where R = response

S =selection differential, calculated from a proportion selected

h^2 = base population heritability

The effects of population structure and selection on expected selection differentials (Hill, 1984b) and base population heritabilities will result in substantial overestimation of the likely rates of response. The use of more complex but more appropriate formulae for predicting responses will lessen the apparent discrepancy between observed and expected responses to selection in sheep populations.

SELECTION FOR BODY CONFORMATION

Leg length in sheep has been traditionally used as a measure of conformation in market lambs. The short cannon bone length typical of terminal sire breeds (for example, Dorset Down) has been viewed as a desirable conformation while the longer cannon bones of crossing ram breeds, or historical long wool breeds, (for example, Border Leicester) have been deemed less desirable. The effects of selection for body conformation on carcase characteristics were examined for these lines by Thorgeirsson (1982). He showed some differences in carcase composition with the long cannon bone line showing slower rates of carcase maturity and therefore lower levels of fatness at a fixed weight than the short cannon bone line. This report has produced evidence for the likely consequences of selection on body conformation in other aspects of productivity.

An initial conclusion was that cannon bone length and body weight were genetically and environmentally related. It was therefore decided to use the phenotypic relationship between the two traits to derive an index of the two traits with the dual aims (Purser, 1960) of:-

* increasing the efficiency of selection by increasing the heritability of the trait
* restricting correlated responses in body weight

(i) Increased heritability. In Chapter 4, the base population parameters of the two traits and the derived index were estimated to examine the likely selection responses. It was concluded that the adjustment of cannon bone length for its phenotypic regression on body weight improved the precision of predicting an animal's genotype by reducing the environmental component of the trait. The direct additive component of the index was relatively higher than the direct additive component of measured cannon bone length and, although the phenotypic variance was reduced, expected genetic responses through direct effects were greater from the index. However, small amounts of additive maternal variance present in both cannon bone length and body weight were also effectively removed by the regression so that total response from both direct and maternal genetic sources was not necessarily enhanced by the use of the index.

(ii) Restricted correlated responses. As shown by Purser (1960), genetic response in body weight would only be zero by selection on the index if the genetic and phenotypic regressions of cannon bone length on body weight were equal. This proved not to be the case with the genetic regression being higher than the phenotypic regression resulting in a positive genetic correlation between the index and body weight. This predicted correlation was fully supported by the observed realised responses to selection.

Thus, the index on which selection was based was neither selection for cannon bone length alone nor selection for cannon bone length with complete restriction on body weight responses. Selection on the derived index resulted in realised direct responses that were close to those expected from base population parameters. The realised responses to selection were slightly lower than the predicted responses, but this difference was accounted for by linkage disequilibrium effects on heritability and lowered response from inbreeding avoidance (Chapter 4). Similarly, the responses in the component traits of the index were extremely close to expectation.

Since the realised responses were well predicted from base population estimates, the consequences of selection on either cannon bone length alone or of a selection index for cannon bone length with restriction on body weight changes can be predicted:-

(i) If selection had been based on cannon bone length, the actual responses would have been of the same magnitude as those observed for cannon bone length as a correlated response to selection on the index. A small part of the overall response would have arisen from maternal genotype. The correlated responses in body weight would have been larger by at least a factor of two.

(ii) Complete restriction of body weight could have been achieved with an index of the form CBL-0.29W compared with the index used of CBL-0.18W (where CBL = cannon bone length and W = body weight, at eight weeks of age). Expected responses in cannon bone length would have been some 25 percent lower than those realised by the index used or expected from selection on cannon bone length above.

Correlated responses to selection on the index were estimated for traits associated with lifetime productivity of hill sheep. Although selection was based on measures of cannon bone length and body weight at eight weeks of age, there was a positive realised genetic correlation between the selected index and body weight at all ages between birth and 5 1/2 years of age. In mice, Rutledge, Eisen and Legates (1974) and Hooper (1977) have observed responses in the length and diameter of long bones as a correlated response to selection on body weight. Similarly, Dawson, Stephenson and Fredline (1972) selected mice on deviations of the length of bones from the regression of bone length on body weight, and observed positive correlated responses in body weight. Such results indicate a general pattern of a genetic association between bone and muscle growth (Hooper, 1977).

Important correlated responses were observed in some components of reproductive performance in this experiment. Litter size, proportion of ewes lambing and lamb survival all showed positive relationships with the index selection. In Chapter 7, these correlated responses were discussed in detail and it was concluded that the responses in reproduction rate were largely a consequence of the responses in body weight. In the mice experiment of Dawson, Stephenson and Fredline (1972), reproduction rate among selected lines also differed (Wodzicka-Tomaszewska, Stephenson and Truscott, 1974). Their 'long' line had both higher litter size and less barrenness than the comparable 'short' line. Again, differences between the lines in body weight largely accounted for this apparent difference in reproduction rate.

Thus, we can conclude that selection can alter the conformation of sheep although the rate of response will depend on whether body weight is also a selection objective. Where selection aims at both increasing body weight and reducing cannon bone length, both traits will respond more slowly to selection because of the unfavourable (positive) genetic correlation between the two objectives. Conversely, selection for increased body weight alone will result in increased cannon bone length. selection for reduced cannon bone length resulted in a substantial decline in overall reproduction rate which would be an undesirable aspect of selection on body conformation. Cannon bone length *per se* was apparently unrelated to aspects of reproductive performance, the correlated responses observed in litter size and lamb survival were probably a function of genetic response in body weight not bone length. Similar evidence from mice would suggest that these conclusions may extend to species other than sheep.

IMPROVEMENT OF SCOTTISH BLACKFACE SHEEP

The hill environment under which Scottish Blackface sheep are expected to survive and produce is extremely harsh. The average productive levels of the unselected control line in Chapter 6 demonstrate some aspects of the environment. For example, body weight growth to maturity showed an irregular pattern with relatively rapid body weight gain during periods of abundant pasture growth in summer and body weight loss during each winter even among young animals. Average levels of reproductive performance were very low with an average litter size of only 1.1 and moderate to high levels of lamb mortality particularly amongst twin born lambs. That this poor reproduction rate was a function of the harsh environment has been demonstrated by the breed comparison of Wiener (1967) who showed an average litter size for Scottish Blackface sheep of almost two lambs per ewe under favourable lowland conditions. Similarly, the average litter size of the experimental sheep in this study increased substantially when moved to an intermediate upland environment (Chapter 7).

The other important feature of Scottish Blackface sheep in their hill environment stems from their behaviour and management. The hefting system operated on hill farms (see Chapter 3) results in groups of ewes occupying relatively confined territories and their female progeny also tending to occupy the same physical environment. The consequences are two-fold:-

(i) Large maternal environmental effects were evident for body weights of lambs. Variation between hefts from such factors as vegetation, shelter or a number of other possible effects resulted in differences between lambs arising from maternal ability of their dams. These differences were relatively large and, in the case of body weight, persisted for a number of years of the animal's life.

(ii) Maternal-direct environmental covariances can arise since daughters and dams share a common environment. This correlation between environmental effects across generations can be closely seen from the higher heritability obtained from daughter-dam regressions (Chapter 4). Purser, Wiener and West (1982) also showed substantial differences between heritabilities estimated from paternal half-sibs and daughter-dam pairs for three dental characters.

It is against this background of environmental and behavioural effects that genetic improvement of Scottish Blackface must be considered.

In Chapter 6, the relevant genetic parameters of lifetime production traits in Scottish Blackface sheep were presented and their implications discussed in detail. The major conclusions of this section only will be restated here together with any modifications arising from the observed correlated responses to selection on adjusted cannon bone length (Chapter 7).

Initially, estimates of genetic parameters from unselected Scottish Blackface sheep were compared with estimates from other unselected breeds in different environments. Important areas of apparent difference were noted for:-

(i) Genetic (co) variance in body weights. It was shown that body weights of lambs up to weaning had very low heritabilities but that post-weaning, the heritability of body weight increased markedly with age to a limiting value of at least 0.3 at maturity. This pattern of age effects was probably a consequence of the large maternal environmental effects operating on the suckling lamb such that the lamb's own genotype had little influence on its body weight up to weaning. Genetic correlations showed a similar trend of increasing covariance between weights with increasing age.

(ii) Genetic variance in reproductive components. Partitioning of reproduction rate into ewe fertility, litter size and lamb survival indicated that useful genetic variance was only apparent in litter size. Yet, selection on adjusted cannon bone length resulted in apparent correlated responses in all three reproductive components (Chapter 7). This disparity will be discussed later in relation to selection objectives for Scottish Blackface sheep.

(iii) The genetic covariance between litter size and adult body weight was very high, particularly in comparison with the low estimates from selected lines (for either litter size or body weight) in other sheep populations.

This variation between population genetic parameters could be due to breed differences, environmental differences or a combination of both effects. However, regardless of their source, it is important that development of breeding plans for Scottish Blackface sheep be based on relevant parameters and that a general solution based on average literature values might not be appropriate.

The economic objective of hill sheep improvement was defined previously (Chapter 6) in terms of reproduction, survival and maintenance of the breeding female and lamb growth. The development of breeding plans involves both genetic considerations (definition of selection criteria) and environmental considerations (management effects on expected responses to selection).

(i) Selection criteria

It was suggested in Chapter 6 that selection for increased reproduction rate should be based on litter size at birth, since genetic variation in ewe fertility and lamb survival was apparently very low. While the correlated responses observed in Chapter 7 indicate that genetic variance in ewe fertility and lamb survival does exist, it is the identification of genetic variation among individuals for these traits which remains difficult. For lamb survival, the results of Cue (1981), indicating a litter size x genotype interaction, and the correlated responses observed here, indicating a maternal age x genotype interaction, are indicative of the problems involved. An indirect selection approach, as advocated by Slee (1981) based on selection for cold resistance, may be useful. Attempting to increase lamb birth weight, either environmentally through the dam or genetically in the lamb, might also be a useful indirect approach since the correlated responses in lamb survival observed in Chapter 7 were largely a function of altered birth weight. However, the effect of maternal age on expected responses and the regular use of fostering as a management procedure will tend to reduce the possible responses to selection.

Likely responses to selection for litter size were presented in Table 6.19 indicating both the high magnitude of potential responses and the opportunity for combining indirect selection (through the high genetic correlation between body weight and litter size) with direct selection on dam's performance. More complex selection indexes using records from other relatives are possible (Martin and Smith, 1980), although in this particular situation they contribute little to accuracy of selection.

Selection for lamb growth is hampered by the low heritability of preweaning body weights and low genetic correlations between preweaning weights and later weights. If selection aimed at both increasing reproductive performance and increasing body weights of lambs, selection on a post-weaning weight would be more rewarding since the correlated responses in preweaning weights would be no lower than direct selection on these weights, and correlated responses in litter size would be much larger (see Chapter 6).

The preceding arguments for selection on body weight in terms of desirable correlated responses in litter size and growth rate are appropriate for the improvement of ewe output. The increased feed requirements for maintenance and production of a larger, more prolific breeding ewe have not been considered. The development of breeding plans for improvement of an economic objective rather than maximising response in output is a more complex question outside the scope of this thesis.

(ii) Management effects

The harshness of the environment and the unique management system used in hill sheep farming have important consequences for genetic improvement programmes. The influence of the hefting system on the expression of maternal effects on lamb body weights has been discussed. Another important result was that small environmental changes in ewe body weight resulted in large effects on both ewe fertility and litter size (Chapter 6). One source of this environmental variation was the influence of previous reproductive performance on body weight at mating, or carry-over effects between parities. With no additional management input such carry-over effects will result in lower than expected rates of genetic response since, for individual ewes, phenotypic superiority at one parity will tend to be reversed at the next parity. In this study, preferential nutrition was routinely offered to ewes rearing twin lambs so that likely carry-over effects for this group of ewes were considerably reduced. It is likely that expected responses to selection for reproductive traits will be highly dependent on the management system adopted in individual situations.

In conclusion, the genetic improvement of Scottish Blackface sheep within a hill farming production system is constrained by the influences of the environment and management. Part of this study has indicated the substantial opportunity that exists for genetic change; the application to specific situations will be, perhaps, more demanding.

BIBLIOGRAPHY

Atkins, K.D. (1980). Selection for skin folds and fertility. Proceedings of the Australian Society of Animal Production. 13 : 174-176.

Avery, P.J. and Hill, W.G. (1977). Variability in genetic parameters among small populations. Genetical Research. 29 : 193-213.

Baker, R.J. and Nelder, J.A. (1978). The GLIM System, Release 3. Numerical Algorithms Group, Oxford.

Baker, R.L., Clarke, J.N., Carter, A.H. and Diprose, G.D. (1979). Genetic and phenotypic parameters in New Zealand Romney sheep. 1. Body weights, fleece weights, and oestrous activity. New Zealand Journal of Agricultural Research, 22 : 9-21.

Becker, W.A. (1975). Manual of Quantitative Genetics. Pullman : Washington State University, 3rd Edition.

Berger, P.J. (1977). Multiple-trait selection experiments. Current status, problem areas and experimental approaches. Proceedings of the International Conference on Quantitative Genetics, Iowa 1976. Eds. E. Pollak, O. Kempthorne and T.R. Bailey, Iowa State University Press, pp. 191-204.

Berger, P.J. and Harvey, W.R. (1975). Realised genetic parameters from index selection in mice. Journal of Animal Science. 40 : 38-47.

Blair, H.T. and Pollak, E.J. (1984). Estimation of genetic trend in a selected population with and without the use of a control population. Journal of Animal Science. 58 : 878-886.

Bradford, G.E. (1972). Genetic control of litter size in sheep. Journal of Reproduction and Fertility, Supplement. 15 : 23-41.

Bulmer, M.G. (1976). The effect of selection on genetic variability : a simulation study., Genetical Research. 28 : 101-117.

Bulmer, M.G. (1980). "The Mathematical Theory of Quantitative Genetics". Clarendon Press, Oxford.

Ch'ang, T.S. and Rae, A.L. (1972). The genetic basis of growth, reproduction and maternal environment in Romney ewes. II. Genetic covariation between hogget characters, fertility and maternal environment of the ewe. Australian Journal of Agricultural Research. 23 : 149-165.

Clayton, G.A., Morris, J.A. and Robertson, A. (1957). An experimental check on quantitative genetical theory. I. Short-term responses to selection. Journal of Genetics. 55 : 131-151.

Clarke, J.N. (1972). Current levels of performance in the Ruakura Fertility flock of Romney sheep. Proceedings of the New Zealand Society of Animal Production. 32 : 94-111.

Cue, R.I. (1981). A genetic analyses of lamb mortality in hill sheep. Ph.D. Thesis, University of Edinburgh.

Cue, R.I. (1983). Correlated responses in lamb mortality due to long term selection for cannon bone length and fleece medullation in sheep. Animal Production. 37 : 293-299.

Cunningham, E.P. and Gjedrem, T. (1973). Genetic control of ewe body weight in selection for higher wool and lamb output. Acta Agriculturae Scandinavica. 20 : 194-204.

Dalton, D.C. and Baker, R.L. (1980). Selection experiments with beef cattle and sheep. In "Selection Experiments in Laboratory and Domestic Animals". Ed. A. Robertson, Commonwealth Agricutural Bureaux, pp. 131-143.

Dawson, N.J., Stephenson, S.K. and Fredline, D.K. (1972). Body composition of mice subjected to genetic selection for different body proportions. Comparative Biochemistry and Physiology. 42B : 679.

Eikje, E.D. (1975). Studies on sheep production records. VII. Genetic, phenotypic and environmental parameters for productivity traits of ewes. Acta Agriculture Scandinavica. 25 : 242-252.

Eisen, E.J. (1967). Mating designs for estimating direct and maternal genetic variances and direct-maternal genetic covariances. Canadian Journal of Genetics and Cytology, 9 : 13-22.

Ercanbrack, S.K., Price, D.A. and Terrill, C.E. (1968). Progress in selecting for overall merit in Ramboiullet sheep. Proceedings of XIIth International Congress of Genetics, Vol. I, p. 275 (abstract).

Falconer, D.S. (1981). "Introduction to Quantitative Genetics". Second Edition, Longman, London and New York.

Forrest, P.A. and Bichard, M. (1974). Analysis of production records from a lowland sheep flock. 3. Phenotype and genetic parameters for reproductive performance. Animal Production. 19 : 33-45.

Gunsett, F.C., Andriano, K.N. and Rutledge, J.J. (1982). Estimating the precision of estimates of genetic parameters realised from multiple-trait selection experiments. Biometrics. 38 : 981-989.

Gunsett, F.C., Andriano, K.N. and Rutledge, J.J. (1984). Estimation of genetic parameters from multiple trait selection experiments. Journal of Animal Science. 58 : 591-595.

Hamilton, B.A. and Langlands, J.P. (1969). Efficiency of wool production of grazing sheep. 1. Differences between Merino sheep selected for high and low fleece weight. Australian Journal of Experimental Agriculture and Animal Husbandry. 9 : 249-253.

Hanrahan, J.P. (1976). Maternal effects and selection response with an application to sheep data. Animal production. 22 : 359-369.

Hanrahan, J.P. (1979). Genetic and phenotypic aspects of ovulation rate and fecundity in sheep. Paper presented to the 21st Poultry Breeders Roundtable, Glasgow.

Hanrahan, J.P. (1984). Results on selection for increased litter size and ovulation rate in sheep. Proceedings of the Second World Congress on Sheep and Beef Cattle Breeding, Pretoria, South Africa, Paper 44, 11pp.

Harvey, W,R. (1977). User's guide for LSML76. The Ohio State University, Columbus.

Henderson, C.R. (1973). Sire evaluation and genetic trends. Proceedings of the Animal Breeding and Genetics Symposium in honor of Dr. J.L. Lush, Blacksburg, Virginia, 1972, pp. 10-41.

Heydenrych, H.J., Vosloo, L.P. and Meissenheimer, D.J.B. (1977). Selection response in South Africa Merino sheep selected either for high clean fleece mass or for a wider S/P ratio. Agroanimalia. 9 : 67-73.

Hill, W.G. (1971). Design and efficiency of selection experiments for estimating genetic parameters. Biometrics. 27 : 293-311.

Hill, W.G. (1972a). Estimation of realised heritabilities from selection experiments. I. Divergent selection. Biometrics. 28 : 747-765.

Hill, W.G. (1972b). Estimation of realised heritabilities from selection experiments. II. Selection in one direct. Biometrics. 28 : 767-780.

Hill, W.G. (1972c). Estimation of genetic change. I. General theory and design of control populations. Animal Breeding Abstracts. 40 : 1-15.

Hill, W.G. (1974). Prediction and evaluation of response to selection with overlapping generations. Animal Production. 18 : 117-139.

Hill, W.G. (1977). Variation in response to selection. Proceedings of the International Conference on Quantitative Genetics, Iowa 1976, Eds. E. Pollak, O. Kempthorne and T.B. Bailey, Iowa State University Press, pp. 343-635.

Hill, W.G. (1978). Design of selection experiments for comparing alternative testing regimes. Heredity. 41 : 371-376.

Hill, W.G. (1980). Design of quantitative genetic selection experiments. In "Selection Experiments in Laboratory and Domestic Animals". Ed. A. Robertson, Commonwealth Agricultural Bureaux, pp. 1-13.

Hill, W.G. (1984a). Detection and genetic asessment of physiological criteria of merit within breeds. In "Genetics of Reproduction in Sheep". Eds. R.B. Land and D.W. Robinson, Butterworths. pp. 319-331.

Hill, W.G. (1984b). Effects of population size on rates and variability of response to short and long term selection. Paper presented to 35th Annual Meeting of the European Association of Animal Production, The Hague, Netherlands.

Hohenboken, W.D. and Brinks, J.S. (1971). Relationships between direct and maternal effects on growth in Herefords. II. Partitioning of covariance between relatives. Journal of Animal Science. 32 : 26-34.

Hooper, A.C.B. (1977). Effects of divergent selection for body weight on bone length and diameter in mice. Animal Production. 24 : 77-82.

Johnson, D.L. (1977). Variance-covariance structure of group means with overlapping generations. Proceedings of the International Conference on Quantitative Genetics, Iowa 1976. Eds. E. Pollak, O. Kempthorne and T.B. Bailey, Iowa State University Press, pp. 851-858.

Koch, R.M. (1972). The role of maternal effects in animal breeding. VI. Maternal effects in beef cattle. Journal of Animal Science. 35 : 1316-1363.

Koch, R.M. and Clark, R.T. (1955). Genetic and environmental relationships among economic characters in beef cattle. III. Evaluating maternal environment. Journal of Animal Science. 14 : 979-996.

Lamberson, W.R. and Thomas, D.L. (1984). Effects of inbreeding in sheep : a review. Animal Breeding Abstracts. 52 : 287-297.

Land, R.B., Atkins, K.D. and Roberts, R.C. (1982). Genetic improvement of reproductive performance. In "Sheep Production". Ed. W. Haresign, Butterworths, pp. 515-535.

Land, R.B., Carr, W.R. and Lee, G.J. (1980). A consideration of physiological criteria of reproductive merit in sheep. In "Selection Experiments in Laboratory and Domestic Animals". Ed. A. Robertston, Commonwealth Agricultural Bureaux, pp. 147-160.

Land, R.B., Gauld, I.K., Lee, G.J. and Webb, R. (1982). Further possibilities for manipulating the reproductive process. In "Future Development in the Genetic Improvement of Animals". Eds. J.S.F. Barker, K. Hammond and A.E. McClintock, Academic Press, Sydney, pp. 59-87.

Latter, B.D.H. and Robertson, A. (1960). Experimental design in the estimation of heritability by regression methods. Biometrics. 16 : 348-353.

McGuirk, B.J (1973). The inheritance of production characters in Merino sheep. Ph.D. Thesis, University of Edinburgh.

McGuirk, B.J. (1980). Selection for wool production in Merino sheep. In "Selection Experiments in Laboratory and Domestic Animals". Ed. A. Robertson, Commonwealth Agricultural Bureaux, pp. 176-197.

McGuirk, B.J., Atkins, K.D., Kowal, E. and Thornberry, K. (1978). Breeding for resistance to fleece rot and body strike - The Trangie Programme. Wool Technology and Sheep Breeding. 26(4) : 17-24.

Mann, T.L.J., Ponzoni, R.W. and Polkinghorne, R.W. (1980). Response to partial selection on clean fleece weight in South Australian strong-wool Merino sheep. V. Estimation of genetic gain by contemporary comparison of progeny of sires two years apart in age. Australian Journal of Agricultural Research. 31 : 1029- 1035.

Mann, T.L.J., Taplin, D.E. and Brady, R.E. (1978). Response to partial selection for fecundity in Merino sheep. Australian Journal of Experimental Agriculture and Animal Husbandry. 18 : 635-642.

Martin, T.G., Sales, D.I., Smith, C. and Nicholson, D. (1980). Phenotypic and genetic parameters for lamb weights in a synthetic line of sheep. Animal Production. 30 : 261-269.

Martin, T.G. and Smith, C. (1980). Studies on a selection index for improvement of litter weight in sheep. Animal Production. 31 : 81-85.

Morley, F.H.W. (1955). Selection for economic characters in Australian Merino sheep. V. Further estimates of phenotypic and genetic parameters. Australian Journal of Agricultural Research. 6 : 77-90.

Morley, F.H.W., White, D.H., Kenney, P.A. and Davis, I.F. (1978). Predicting ovulation rate from liveweight in ewes. Agricultural Systems. 3 : 27-45.

Mueller, J.P. (1983). Population structure and selection criteria in animal breeding programs. Ph.D. Thesis, University of New South Wales.

Newman, J.A., Rahnefeld, G.W. and Fredeen, H.T. (1973). Selection intensity and response to selection for yearling weight in beef cattle. Canadian Journal of Animal Science. 53 : 1-12.

Nicholas, F.W. (1980). Size of population required for artificial selection. Genetical Research. 35 ; 85-105.

Nicholas, F.W. (1981). The effect of replication on response to selection. Proceedings of the Second Conference of the Australian Association of Animal Breeding and Genetics, pp. 250-251.

Osman, A.H. and Bradford, G.E. (1965). Effects of environment on phenotypic and genetic variation in sheep. Journal of Animal Science. 24 : 766-774.

Pattie, W.A. (1965). Selection for weaning weight in Merino sheep. 1. Direct response to selection. Australian Journal of Experimental Agriculture and Animal Husbandry. 5 : 353-360.

Pattie, W.A. and Barlow, R. (1974). Selection for clean fleece weight in Merino sheep. I. Direct response to selection. Australian Journal of Agricultural Research. 25 : 643-655.

Pattie, W.A. and Trimmer, B. (1964). The milk production of Merino ewes from flocks selected for high and low weaning weight. Proceedings of the Australian Society of Animal Production. 5 : 156-159.

Piper, L.R. and Bindon, B.M. (1977). The genetics of early viability in Merino sheep. Proceedings of the Third International Congress of the Society for the Advancement of Breeding Researches in Asia and Oceania (SABRAO), Canberra, Animal Breeding Papers, pp. 10.17-10.22.

Piper, L.R. and Bindon, B.M. (1982). Genetic segregation for fecundity in Booroola Merino sheep. Proceedings of the World Congress on Sheep and Beef Cattle Breeding, Palmerston North, New Zealand. Eds. R.A. Barton and W.C. Smith, The Dunsmore Press, Vol. I, pp. 394-400.

Piper, L.R. and Dolling, C.H.S. (1969). Efficiency of conversion of food to wool. IV. Comparison of sheep selected for high clean wool weight with sheep from a random control group at three levels of dietary protein. Australian Journal of Agricultural Research. 20 : 561-578.

Purser, A.F. (1960). The use of correction for regression on a second character to increase the efficiency of selection. In "Biometrical Genetics". Ed. O. Kempthorne, Pergamon Press, pp. 210-214.

Purser, A.F. (1965). Repeatability and heritability of fertility in hill sheep. Animal production. 7 : 75-82.

Purser, A.F. (1967). Selection experiments with hill sheep. Proceedings of the Ninth International Congress of Animal production, Edinburgh, 1966. pp. 32-38.

Purser, A.F. (1980). Comparison of expected and realised responses in three sheep selection experiments. In "Selection Experiments in Laboratory and Domestic Animals". Ed. A. Robertson, Commonwealth Agricultural Bureaux, pp. 21-30.

Purser, A.F. (1982). Implications of sheep selection experiments. Proceedings of the World Congress on Sheep and Beef Cattle Breeding. New Zealand. Eds. R.A. Barton and W.C. Smith, The Dunsmore Press, Vol, I, pp. 239-248.

Purser, A.F. and Roberts, R.C. (1964). The effect of treatment during first winter on the subsequent performance of Scottish Blackface ewes. Animal Production. 6 : 273-284.

Purser, A.F., Wiener, G. and West, D.M. (1982). Causes of variation in dental characters of Scottish Blackface sheep in a hill flock, and relation to ewe performance. Journal of Agricultural Science. 99 : 287-291.

Rae, A.L. (1958). Genetic variation and covariation in productive characters of New Zealand Romney Marsh sheep. New Zealand Journal of Agricultural Research. 1 : 104-123.

Richardson, R.M., Kojima, K. and Lucas, H.L. (1968). .An analysis of short term selection experiments. Heredity. 23 : 493-506.

Robards, G.E. and Pattie, W.A. (1967). Selection for crimp frequency in the wool of Merino sheep. 1. Direct response to selection. Australian Journal of Experimental Agriculture and Animal Husbandry. 7 : 552-558.

Robertson, A. (1959). Experimental design in the evaluation of genetic parameters. Biometrics. 15 : 219-226.

Robertson, A. (1962). Weighting in the estimation of variance components in the unbalanced single classification. Biometrics. 18 : 413-417.

Robertson, A. (1977a). The effect of selection on the estimation of genetic parameters. Zeitschrift fur Tierzuchtung und Zuchtungsbiologie. 94 : 131-135.

Robertson, A. (1977b). Artificial selection with a large number of linked loci. Proceedings of the International Conference on Quanatitative Genetics, Iowa 1976. Eds. E. Pollack, O. Kempthorne and T.B. Bailey, Iowa State University Press, pp. 307-322.

Robertson, A. and Lerner, I.M. (1949). The heritability of all-or-none traits : viability of poultry. Genetics. 34 : 395-411.

Rutledge, J.J., Eisen, E.J. and Legates, J.E. (1974). Correlated response in skeletal traits and replicate variation in selected lines of mice. Theoretical and Applied Genetics. 45 : 26-31.

Saville, D.G. and Robards, G.E. (1972). Efficiency of coversion of food to wool in selected and unselected Merino types. Australian Journal of Agricultural Research. 23 : 117-130.

Shelton, M. and Menzies, J.W. (1970). Repeatability and heritability of components of reproductive performance in fine-wool sheep. Journal of Animal Science. 30 : 1-5.

Slee, J. (1981). A review of genetic aspects of survival and resistance to cold in newborn lambs. Livestock Production Science. 8 : 419-429.

Soller, M. and Genizi, A. (1967). Optimum experimental designs for realised heritability estimates. Biometrics : 23 361-365.

Thorgeirsson, S. (1982). Growth and development of Scottish Blackface and Icelandic sheep. Ph.D. Thesis, University of Edinburgh.

Tsiatis, A.A. (1980). A note on a goodness-of-fit test for the logistic regression model. Biometrika. 67 : 250-251.

Turner, H.N. (1977). Australian sheep breeding research. Animal Breeding Abstracts. 45 : 9-31.

Turner, H.N. (1978). Selection for reproduction rate in Australian Merino sheep. Direct responses. Australian Journal of Agricultural Research. 29 : 327-350.

Turner, H.N., Brooker, M.G. and Dolling, C.H.S. (1970). Response to selection in Australian Merino sheep. III. Single character selection for high and low values of wool weight and its components. Australian Journal of Agricultural Research. 21 : 955-984.

Turner, H.N., Dolling, C.H.S. and Kennedy, J.F. (1968). Response to selection in Australian Merino sheep. I. Selection for high clean fleece weight, with a ceiling on fibre diameter and degree of skin wrinkle. Response in wool and body characteristics. Australian Journal of Agricultural Research. 19 : 79-112.