

LONG TERM SELECTION EXPERIMENT WITH SHEEP

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SUMMARY

This review summarises direct and correlated responses in sheep selection experiments. Realised heritabilities from flocks selected for between 9 and 21 years show reasonably good agreement with heritabilities in the base population. In none of the flocks was there convincing evidence of a selection plateau. The value of these selection flocks for studying correlated responses is illustrated by reference to flocks selected for increased wool production. These have been used to examine correlated changes in efficiency of feed conversion, and related physiological topics, and to examine possible changes in the processing properties of wool.

INTRODUCTION

Selection experiments have been used extensively to study the quantitative genetics of sheep populations. Their first reported use was just prior to the 1950s, at a time when such experiments were not widespread, even with laboratory animals. Atkins (1985) has estimated that possibly 60 such experiments have been reported, and the majority have been described in reviews by Dalton and Baker (1980), Purser (1982), McGuirk (1983) and Land et al. (1983). Here we have interpreted the description 'long-term' rather liberally, to cover experiments spanning as few as 10 years, which is often equivalent to only three generations of selection.

USES OF SELECTION EXPERIMENTS

Sheep selection experiments were established or have been used for many of the same general reasons listed by Hill (1980).

1) To provide an experimental check on theoretical predictions of progress in both selected and correlated traits.

Many of the early sheep selection studies were established with the specific aim of providing some experimental validation of selection theory; to see if it actually "worked" for characters of economic importance in a commercial livestock species. A quantitative check of theory would require estimates of realised heritabilities and genetic correlations, which could then be compared with estimates in the base or unselected population. Table 1 summarises those studies in which realised and estimated heritabilities have been compared. In many more studies such a comparison cannot be made, because of incomplete data analysis, the lack of parameter estimates for the base population or because the selection procedure followed meant response could only be predicted very approximately. Nevertheless, we will endeavour to summarise the major conclusions of these studies.

2) To determine how long predicted or initial rates of response are maintained. The estimation of realised genetic parameters is most appropriately a feature of short-term selection responses. For long-term experiments, our interest turns increasingly to selection limits, if and when they occur. Given

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that the longest sheep selection experiment has run for less than 15 generations, it would be somewhat unexpected to find that response had stopped in that time, unless very few genes are involved, or some form of scale effect was operating and/or the biological limit to expression had been reached.

3) Symmetry of direct and correlated responses. Theory would predict equal genetic gains, both direct and correlated, regardless of whether selection was for increased or reduced expression of a character. Many sheep selection studies have included both divergent lines and a control, so that the symmetry of response can be tested. By contrast with studies of laboratory animals, asymmetric responses with sheep and other farm livestock can have important practical and economic implications.

4) Comparison of alternative selection methods. This has generally not been a major objective. In one of the early Australian experiments for increased fleece weight, selection in one flock was based on a combination of individuals and half-sib information (Turner et al. 1968). In two other experiments with Australian Merinos, gains in a flock selected primarily on measurement were compared with those achieved by selection solely on a visual assessment of merit, the traditional approach to improving wool production (Gregory and Ponzoni, 1981; McGuirk, 1983).

5) Study of genotype x environment interaction. If lines are selected and tested for the same trait in two different locations, it is possible to estimate realised heritability in each environment and the genetic correlation. A less extensive measure of genotype x environment interactions can be obtained by testing lines selected in a single environment in a number of different environments.

6) To provide information on possible correlations between the trait under selection and other characters, where we have no prior information on the genetic correlation. Within this general description we could include:

a) Efficiency studies: While selection is for increased production per head, production per unit of land or feed input, two measures of efficiency of production, may be related more closely to profitability.

b) Product quality: Selection for increased growth and wool production could affect the quality of the end-products.

c) Physiological understanding: Flock selected for different production characters have been widely used for physiological studies. In addition to a general interest in elucidating the physiological basis for genetic differences in production, there is often a specific interest in identifying indirect selection criteria, traits which might be more useful as a basis for selection than the character which we wish to improve. This is especially true for ewe reproductive performance (see Walkley and Smith, 1980), a sex-limited trait which is also often restricted in expression to a small number of classes.

DESIGN AND ANALYSIS OF EXPERIMENTS

Despite the multiplicity of specific objectives in establishing selection experiments, we are ultimately concerned with the measurement of a selection response, from which we wish to estimate realised genetic parameters. We also want an estimate of the precision of these responses and genetic parameters. All of these are influenced by the design of the experiment, by the size of the selection flocks, if they are replicated, the intensity of selection, the duration of the experiment and the procedure used to measure responses. We will provide a brief summary of the design factors of sheep selection experiments, emphasising how they differ from similar studies with laboratory animals.

Size and Age Structure and Replication

Sheep selection flocks vary in size. Flock sizes have varied from as few as 30 ewes, mated each year to 1-2 rams (Turner et al., 1970), up to a maximum of 200 ewes mated each year to 20 rams. The pattern of using many fewer males than females is general, and reflects the different reproductive potential of the two sexes. Commonly, both the rams and ewes in the selection flocks have been of mixed ages. For the ewes, this is very often a necessary situation, brought about by their low reproductive potential, and hence the need to retain them in the flock for two and often more lambings. For the males, the age structure is usually chosen so as to maximise annual genetic progress, generally a compromise between maximising selection differential and minimising generation length. Because the flocks are of mixed ages, we finish up with overlapping generations and this presents difficulties when predicting and measuring responses to selection, and in estimating effective population size and the expected variance of responses.

We know of no replicated flocks that were selected in an identical manner from the same base population. For this reason, it is not possible to use the observed variation among replicates as our measure of the variance of response to selection. Instead, the variance has to be arrived at from predictions of genetic drift and measurement error (Hill, 1972a, b). A number of Australian Merino flocks have been established with similar selection criteria from similar base populations. While not replicates in any strict sense, their average rates of response and the general pattern observed in some of the correlated responses increases our confidence as to the general nature of any changes observed.

Measurement of Response

One important feature of sheep selection experiments is that sheep are exposed to environmental influences which can vary widely, with a corresponding effect on performance. Robards (1979) found the between year coefficient of variation for fleece weight in a number of unselected Merino flocks to average 20 per cent. Any attempt to measure responses to selection should account for such year to year fluctuations in performance, as well as any long-term change in environmental conditions.

The most commonly used method of separating genetic and environmental changes, and so measure responses to selection, is by the use of a randomly selected control line. This provides a continuous measure of the environment for all measured characters, from which genetic changes, both direct and correlated, can be assessed. While such a control line will require considerable resources to maintain and measure, a single control can be used for more than one selection line. Control flocks have the important extra value of providing information on genetic variances and covariances, without the complicating effects of selection. Often the control flock will be larger than the selection flocks, or use more males for mating, to reduce genetic drift. However, this is likely to give rise to different rates of inbreeding in the selected and control populations.

In future it will be possible to use frozen semen or embryos, to provide an occasional measure of responses. The former method has been simulated by the repeat mating method, in which contemporary comparisons were made of the progeny of old and young sires (Mann, Ponzoni and Polkinghorne, 1980). Using live rams has the important limitation of ram longevity. Unless the sires are markedly different in age, the expected differences between the progeny groups are small and imprecisely measured.

When one attempts to compare the progeny of young and older rams on a continuing basis, there is the difficulty either of slowing the rate of response in the experiment, by increasing generation lengths, or having to find additional resources outside the selection flock itself, to measure change. Commonly, the same rams will be included as young and old rams in different years. This suggests that mixed model statistical procedures could and should be used in such circumstances, to estimate year of birth effects from sire breeding values. Use of information on the genetic relationships among animals could also be attempted, and no doubt will be in future studies designed to measure genetic change in selection experiments. Whether it can also be used to estimate realised genetic parameters, as proposed by Blair and Pollak (1984), is questionable (Thompson, 1986).

Prediction of Response

Response is usually predicted as a function of the selection differential and the heritability of the trait. However, with overlapping generations, this prediction only holds asymptotically. Hill (1974) has described a matrix method for predicting genetic change on an annual basis, taking account of the net contribution of genes of each age group of parents to successive groups of progeny (See Mann, Taplin and Brady, 1978).

In practice, it is customary to estimate cumulative selection differentials for each individual. Realised genetic parameters are then estimated by regression procedures, as described by Turner and Young (1969) and Barlow (1974). For example, realised heritability can be estimated as the regression of cumulative response on cumulative selection differential. For a particular group of progeny, response is simply the departure in performance from the control flock. The corresponding selection differential is the average cumulative selection differential of their parents. Calculating an achieved selection differential has the advantage of accounting for variable individual reproductive performance and fluctuations in selection intensity. It also enables selection differentials to be scaled as a possible approach to account for genotype x environment interactions (Pattie, 1965). Recently, James (1986) has shown that the procedure generally used to estimate cumulative selection differentials in sheep selection studies (see Pattie, 1965) is incorrect, so that cumulative selection differentials have been over-estimated, and realised heritability values correspondingly under-estimated. In the cannon bone selection experiment described by Purser (1980, 1982), Atkins (1985) has shown that the incorrect method over-estimated the cumulative selection differential by up to 15-20 per cent.

Precision of Estimates

An important consideration in any selection experiment is the sampling variance of realised genetic parameters. Many of the published estimates of standard errors from sheep selection experiments have not allowed for the effect of drift variance. Drift variance arises principally from the genetic sampling of individuals from one generation to become the parents of the next generation. It thus accumulates across generations. By contrast, measurement error variance, the other contributor to the expected variance of response, does not accumulate, and in each generation is a function of the number of animals measured. With time, drift variance dominates the overall variance of response.

Table 1. A comparison of realised and base population heritability (h^2) estimates from single trait selection experiments in sheep.

Expt	Trait selected (breed)	Duration in years (generations)	Realised h^2 (\pm s.e.)	Base population h^2	References (see below)
<u>Fleece weight</u>					
1	- Aust Merino	14 (5)	0.24 \pm .04*(high)	0.47	8,6
2	- NZ Romney	21 (9)	0.15 \pm .04(high)	0.31	3
3	- SA Merino	13 (5)	0.24 \pm .07*(high)	0.31	4
<u>Follicle Fleece</u>					
4	- SA Merino	13 (5)	0.34 \pm .13*	0.50	4
<u>Crimp Frequency</u>					
5	- Aust Merino	14 (5)	0.46 \pm .03*	0.47	6,11
<u>Weaning Weight</u>					
6	- Aust Merino	10 (4)	0.25 \pm .03*	0.18	7
7	- Cheviot	9	0.24 \pm .11(high)	0.19	10
<u>Cannon bone length</u>					
8	- Scottish Blackface	19 (8)	0.49 \pm .02†	0.54	1,9
<u>Medullation Index</u>					
9	- Scottish Blackface	19 (8)	0.45 \pm .03	0.48	9
<u>Skin Wrinkle</u>					
10	- Aust Merino	19 (7)	0.36 \pm .04	0.50	5,6
<u>Face Cover</u>					
	- NZ Romney	21 (9)	0.48 \pm .06	0.30	2

References: 1. Atkins (1985), 2. Blair et al. (1984), 3. Blair et al. (1985), 4. Heydenrych, Vosloo and Meissenheimer (1984), 5. McGuirk (1973), 6. Morley (1955), 7. Pattie (1965), 8. Pattie and Barlow (1974), 9. Purser (1980), 10. Purser (1982), 11. Robards and Pattie (1967).

* Approximate standard errors estimated from published data using the formulae of Hill (1972a, b).

† Standard error incorporates drift variances as for overlapping generations (Johnson, 1977).

In summarising estimates of realised heritability, we have attempted to allow for the contribution of both drift variance and measurement error, using formulae given by Hill (1980). These use information on effective population size, duration of the experiment, selection intensity and expected genetic

variances or covariances. Some of these have had to be guessed at. Effective population sizes were calculated as described by Hill (1972c) for populations with overlapping generations. As in the case of expected responses to selection, the expressions described by Hill (1980) for drift variances are only asymptotically true when generations overlap. Johnson (1977) has provided more exact formulae for the case of overlapping generations, and showed that drift in the early years of an experiment are larger than predicted using the discrete generation formulae. This is well illustrated in Figure 1, taken from Atkins (1985), which indicates how failure to allow for drift variance underestimates the expected variance in response.

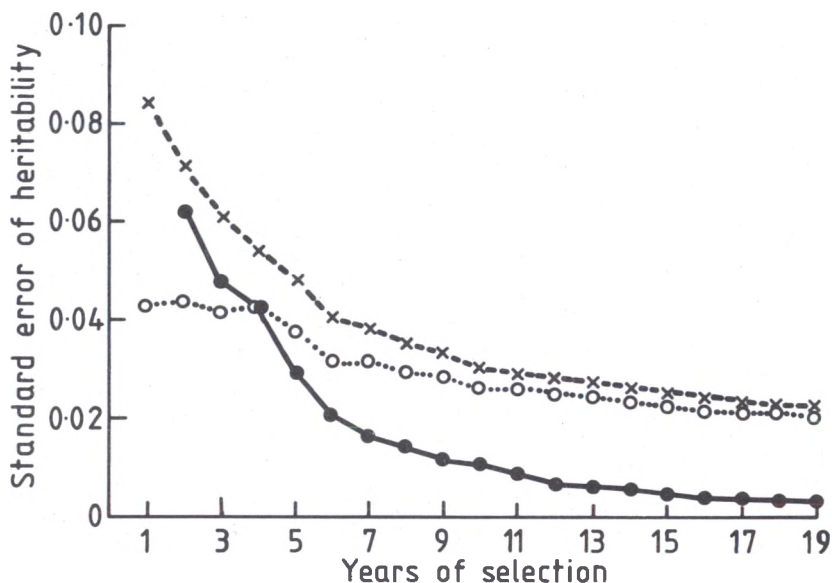


Fig. 1. Apparent sampling variances of realised heritability (from Atkins, 1985).

x---x Including drift calculated as for overlapping generations
 o---o Asymptotic drift assumed
 o—o Drift ignored

RESULTS OF THE EXPERIMENTS

In reviewing this information, we will use the same headings as used previously when discussing reasons for establishing sheep selection experiments. For convenience, we will firstly consider aspects of direct selection; agreement between predicted and realised responses, linearity and duration of responses, symmetry of responses and comparison of alternative selection methods; discuss genotype x environment interactions, and then discuss correlated responses.

Direct responses to selection

In Table 2.1 we have listed single trait sheep selection lines which yielded an estimate of realised heritability and where a heritability estimate was also available for the base population. The estimates of realised heritability given refer to divergent selection, unless stated otherwise.

All of the traits considered had a moderate to high heritability. In general the estimate of realised heritability was slightly smaller than the base population estimate. This could be due in part to the overestimation of selection differentials in most of these studies (James, 1986). Selection itself would be expected to lead to a reduction in heritability, by generating negative linkage disequilibrium (Bulmer, 1980). These considerations apply to all of these selection experiments. However, if we group the experiment according to the character under selection, we can see that those for fleece weight are consistently below expectations. This is especially apparent if we consider only the upward selection line in Experiment 1, along with the unidirectional Experiments 2 and 3. This pattern may reflect the long history of selection for increased fleece weight in these populations/breeds. By contrast, gains in the two flocks selected for weaning weight (Expts. 6 and 7), gave realised heritability estimates that were higher than the corresponding paternal half-sib estimates. The discrepancy in Expt. 6 is probably due to maternal genetic effects, reflecting a positive genetic correlation between weaning weight and milk production in the ewe (Pattie and Trimmer, 1964). Offspring-dam heritability estimates were higher than paternal half-sib estimates for weaning weight in this population (Pattie, 1965).

The only experiment which uses appropriate procedures for calculating cumulative selection differentials (James, 1986), and incorporating drift variances is the cannon bone selection study (Atkins, 1985), previously described by Purser (1980, 1982). After allowing for the degree of within family selection that was practised, the realised heritability to divergent selection of 0.52 (± 0.02) was slightly and non-significantly less than the heritability of 0.56 (± 0.04) in the base and control populations. The agreement between the two is more remarkable if allowance is made for the reduction in heritability in the selected population due to linkage disequilibrium (Bulmer, 1980).

Land et al. (1983) summarised the results of selection for increased reproductive performance. The selection criteria employed varied from litter size to numbers of lambs weaned per ewe joined (mated). Predictions of response were generally made difficult by the lack of an adequate set of genetic parameters for the population. Despite these difficulties the average rate of response of two per cent per year was in good general agreement with predictions.

A group of multi-trait Merino selection flocks (see McGuirk, 1983) represent another group of experiments where it is not possible to confidently predict a rate of response. The major aim in all was to increase clean fleece weight, and gains of 1.5-2.0 per cent per year in this character were anticipated. Gains observed over periods of 20-25 years averaged close to one per cent (McGuirk, 1983).

Symmetry, Linearity and Duration of Response

Symmetry of responses have been examined in Experiments 1, 5, 6 and 10 of those listed in Table 1. In Experiment 1, realised heritability to downward

selection was similar to the base population heritability while heritability to upward selection was appreciably less. Responses to upward and downward selection were similar for both crimp frequency and weaning weight (Expts. 5 and 6 respectively). There have been few formal studies on the linearity of responses in sheep selection data. Purser (1980, 1982) commented on the good agreement between predicted responses and those achieved over the duration of experiments while Atkins (1985) found no significant quadratic effect when testing cumulative response on cumulating selection differentials in the cannon-bone selection line (Expt. 8). Adequate tests of symmetry and linearity should allow for possible effects of inbreeding on performance and the expected reduction in heritability, and hence response, due to linkage disequilibrium.

There were suggestions that initial rates of responses were not maintained in a number of the multi-trait flocks selected primarily for increased fleece weight (Turner et al., 1968), but no attempt was made to relate the gains to achieved selection differentials. Pattie and Barlow (1974) suggested an early plateau to upward selection in Expt. 1. However, while gains in this flock are below expectation (McGuirk, 1983), they have not ceased. Rogan (1984) estimated an annual rate of improvement over the period 1968-1981 of approximately 0.7 per cent per year, over the period of from 6 to 10 generations of selection.

It is a moot point as to what general conclusion would be drawn if a selection plateau could be demonstrated in a selection flock. Given the small size of these flocks, with the consequent increases in inbreeding, it is not clear if any physiological or genetic limits observed would have general relevance to much larger industry flocks.

Relative Efficiency of Different Selection Methods

In two long-term experiments with Australian Merinos, selection based on measurement or visual assessment were compared, in the hope that selection on measurement would be more effective in increasing fleece weight. At Trangie, over a twenty year period, annual gains in fleece weight were 1.03 per cent per year in the flock where measurement was used, compared with 0.49 per cent per year where replacements were selected visually (McGuirk, 1983). In the second experiment selection based on measurement was also more efficient, and average fleece weights in the two flocks diverged by approximately one per cent per year (Gregory and Ponzoni, 1981).

Genotype x Environment Interactions

There have been a number of studies in which responses from a selection flock have been measured in different environments. In studies involving flocks selected for aspects of wool production, the environments have commonly involved altering the nutritional regime (see McGuirk, 1983). While almost all were successful in demonstrating a statistically significant flock x nutritional environment interaction, in none of these studies was there a change in rank. The superiority of the high fleece weight selection flock, over either the control flock or low fleece weight flock animals, increased as the average level of wool production increased. This form of interaction is also observed if production is measured at different sites on the sheep (McGuirk, 1983).

CORRELATED RESPONSES

In our Introduction, we listed a number of reasons why correlated responses are of interest in sheep selection studies. Where prior information on genetic correlations is available, we are particularly interested in checking

correlations between pairs of important production characters. In monitoring physiological consequences of selection, and possible changes in product quality, we are generally operating without prior information.

Agreement Between Predicted and Realised Correlations

Testing the agreement between predicted and realised correlations is complicated by the fact that correlation estimates for the unselected population are often subject to large sampling errors, much more so than for heritability estimates. Realised correlations have been calculated using regression procedures (see Turner and Young, 1969), while Barlow (1974) attempted to allow for non-linear responses (Expt. 1) in the character under selection. Generally no account has been taken of drift variances.

Selection for fleece weight show good agreement between estimated and realised genetic correlations, as McGuirk (1983) showed in summarising the correlations presented by Barlow (1974). The same pattern can also be seen in papers by Heydenrych et al. (1984) and Blair et al. (1985). However, important discrepancies are apparent if we compare expected and realised correlations when selection was for the components of fleece weight (average fibre diameter, wool follicle characters etc.) when attempting to improve fleece weight itself (Turner, Brooker and Dolling, 1970; Rendel and Nay, 1978). It is interesting to speculate on how well genetic correlation estimates provide an adequate general description of correlated changes involving composite traits and their components.

Physiological Studies and Product Quality

Wool. The most extensive investigation of physiological responses to selection have involved flocks selected for aspects of wool production. These studies have been reviewed extensively by Williams (1979) and McGuirk (1980, 1983) and will only be summarised briefly here. The fact that similar findings were observed with a number of different selection flocks has greatly increased confidence as to the general nature of these findings.

There have been numerous studies on the efficiency of conversion of feed to wool using animals sampled from selection and control flocks. Fleece weight and body weight have a negligible genetic correlation, and the gains in fleece weight in the single trait selection flocks have been shown to be due almost entirely to an increase in efficiency, and not in feed intake. In some of the multitrait selection flocks, where there have been gains in body weight as well as fleece weight, there have still been substantial benefits in feed efficiency (see Williams, 1979). Selection for increased fleece weight appears to have improved the utilization of nutrients after absorption from the alimentary tract. Most research in this area focussed on the metabolism of cystine, as wool contains a high proportion of this sulphur-containing amino acid, and because wool growth is increased by abomasal and intravenous infusion of this and related amino acids. However, it is not clear how selection has altered cystine metabolism (Williams 1979). Blood plasma cystine levels are reduced by selection, probably accounting for the lower concentration of sulphur in wool of sheep from high fleece weight selection flocks. These sheep are also more responsive to infusions of cystine or methionine, and show a greater increase in wool growth and sulphur output than sheep from low fleece weight selection flocks (see McGuirk, 1983).

Wools from selection flocks can also be used to monitor possibly undesirable effects on the physical and chemical properties of wool, which could

influence their processing performance or consumer acceptability. Recent studies on flocks selected solely for increased fleece weight showed the expected increases in average fibre diameter and fibre length and a reduction in resistance to compression; characteristics of importance in all end-uses for wool (see McQuirk, 1983). Changes in the variation in fibre diameter and in scoured colour were small (McQuirk et al., 1984). Provided average fibre diameter is kept constant, as is recommended in commercial breeding programmes, only small changes in processing performance of Merino type wool will result from selection for fleece weight.

Lipson and Walls (1962) examined the worsted manufacturing performance of wools from a multi-trait selection flock where the major emphasis was on increasing fleece weight (Turner et al., 1968). The gains in fleece weight in this experiment were achieved without increasing average fibre diameter. Wool from the high fleece weight flock was superior in a number of processing stages and both the yarn and cloth were of greater strength than wool from the control flock.

Growth and Development: Recently Thompson and his co-workers described the effects on feed efficiency, growth, and development of selection for weaning weight in Merino sheep (see Thompson et al., 1985a, b, c). Selection increased body weight at all ages, including mature weight. Selection increased food intake (appetite) in the early stages of growth. While the gross food conversion efficiency was not altered at a given age, sheep from the high weight selection flock were more efficient at a given weight. At a given proportion of mature weight, the high body weight selection group still had a greater feed intake in early life, and also reached a greater proportion of their mature size at a given age. Subsequently, Thompson and Kinghorn (1985) have examined the broader implications of these results on the efficiency of the ewe-lamb meat production unit.

The process of development was also altered by selection. Selection for increased weaning weight also increased the proportion of bone and ash in the body of mature animals, with the high body weight line having the greatest proportion of bone and ash and less fat. Selection also altered the rate of deposition of fat such that at low body weights, they had a higher proportion of fat. In carcass studies on lambs from the cannon-bone length selection lines (Expt. 8), Thorgiersson (1981) concluded that selection for short cannon-bone, traditionally associated with a desirable carcass type, produced a carcass which at any given weight contained more fat and showed greater development of the later maturing joints.

Reproduction: The selection criteria used in the flocks selected for reproduction have varied from litter size to number of lambs weaned per ewe joined (mated). This variation complicates any discussion of correlated response, as different components of reproduction could contribute to overall responses. Where selection has been solely or primarily for increased litter size, the gains would appear to be due almost entirely to increased ovulation rate (see Hanrahan, 1984). Where selection was for increased numbers of lambs weaned, both litter size and lamb survival improved (Atkins, 1980).

To date there is little information on the effect that improving reproduction has on the efficiency of production. Mature ewe weight has shown little or no increase in lines selected for increased multiple births (Bradford, 1985), so that maintenance feed requirements are likely to be little affected. However, feed requirements would be increased during pregnancy and lactation as litter sizes increase.

Surprisingly few physiological studies have been made on these flocks. The stimulus for much of the study of endocrinological and morphological features of flocks that differ in reproduction has been the desire to identify selection criteria among young males that could be used to improve the reproductive performance of their daughters. To date, this research has proved unsuccessful as regards FSH and LH levels (Findlay and Bindon, 1976). Similarly, flocks selected for testis size (Lee and Land, 1985) have not produced correlated changes in ewe reproductive performance. Findlay and Bindon (1976) did report differences in FSH levels between ewes sampled from a high twinning flock and its control. Ricordeau et al. (1984) have also reported a positive genetic relationship between FSH levels in young ewes and the breeding values of their sires for reproduction.

CONCLUSIONS

From our survey of sheep selection experiments, it is clear that they have been widely used to study genetic variation and covariation in sheep populations. Despite the difficulties of long generations and fluctuating environments, the economic importance of the species itself and the characters studied has obviously provided a major boost to such investigations, and added significance to any findings they may produce. At the same time, it is regrettable to note that many of these experiments have as yet been reported in only a descriptive or semi-quantitative fashion.

While selection experiments are only one of a number of possible approaches to the study of quantitative inheritance, they are especially useful in providing general description of the long-term effects of selection. Because of their small size they may not be particularly appropriate in predicting limits to selection in breeds where the effective population size is usually much greater. However the existence of selection flocks has made it possible to look at long-term consequences of selection for fleece weight and chemical and physical properties of wool and on its processing performance. Their existence has also made it financially feasible to examine the effects of selection for increased fleece and body weight on the efficiency of feed conversion. The possibilities they offer for further detailed biological and physiological understanding is a strong argument for the maintenance of such flocks, and the establishment of further flocks selected for characters of major economic significance. A similar argument can be made for maintaining multi-trait selection flocks which mimic currently recommended industry selection practices, even if such flocks may not be suitable for estimating realised genetic parameters. Those can provide early evidence of possibly undesirable changes that might occur in industry improvement programmes.

The design of selection experiments can have a critical effect on the value of selection experiments as quantitative tools, as it will affect the sampling of all realised parameters. This is clearly of relevance when comparing realised responses with predictions, but also when we have no prior information on possible correlated changes. There is little point in screening for possible indirect selection criteria if we then have little confidence in the estimates of genetic covariances is obtained. Sampling variances can be predicted in advance for different population structures and selection strategies (Johnson, 1977) so that likely sampling variances can be anticipated. With the recent extension of design considerations to cover multivariate selection (see Cameron and Thompson, 1986), selection experiments are likely to play an even greater role in sheep breeding research.

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