

Breeding Plans for Sheep - Past and Possible Progress

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SUMMARY

THIS paper outlines the general structure of the Merino industry in Australia, and reviews its influence on plans for genetic improvement. Various mating plans are discussed, and the conclusion reached that mass selection on measured phenotype has a wide general application. Further information is required, however, as to the extent to which environment may alter ranking on performance.

I. INTRODUCTION

Various breeding plans are available to animal breeders, and the choice of a plan is influenced by many factors, including the type of animal and the particular aspect of its performance in which the breeder is interested. This paper is designed to review briefly the factors which govern the choice of a plan in relation to sheep-breeding for wool production, particularly under Australian conditions. There will be discussion of existing knowledge concerning theoretical and practical points which have a bearing on the decision, as well as an indication of need for further research.

In defining a breeding problem with any animal, the first step is to obtain a general description of the breeding structure of the industry, together with its method of husbandry and its vital statistics. Next comes the problem of defining "performance" - that is, establishing the criteria for assessing the type of production with which the breeding plan is to be concerned. The breeding plan itself will then cover the two processes of selection and mating, which are sometimes, though not always, distinct. Some aspects of the two processes can be made clearer if they are discussed separately.

II. DESCRIPTION OF THE AUSTRALIAN WOOL-GROWING INDUSTRY

(a) Breeding structure

For present purposes, discussion will be confined to the Merino industry, which contributes the major part of Australian wool production. The Merino population is in two sections - commercial flocks, whose main product is wool, and registered studs, whose main product is breeding stock. Short and Carter (1955) have analysed the flock records of the registered studs, as published annually in the "Australian Stud Merino Flock Register". They have outlined a structure commencing with 24 closed "parent" studs, mating some 164,000 ewes, from which stock migrate to two other types - "daughter" studs, dependent on one "parent" only, and "general" studs, dependent on more than one "parent". In 1950 there were 258 daughter studs, mating 220,000 ewes, and 685 general studs, mating 497,000 ewes.

Annual ram replacements for the non-registered flocks are supplied partly from the non-registered flocks themselves, but are also drawn from the registered studs; Short and Carter give estimates of the proportion from the latter, which vary from 50 per cent. in some years to as high as 90 per cent. in others. Of this, the parent and daughter studs contribute some 25 per cent., and the general studs the remainder. In the existing records there appears to be no way of determining the proportion of non-registered flocks which draw their rams consistently from the same source.

The size of a flock has a direct bearing on the type of breeding plan which might be considered, and on the amount of genetic progress which might be made. Short and Carter do not present a complete distribution of registered studs according to flock size, but they quote the mean size in 1950 as 6,842 ewes for parent, 852 ewes for daughter and 726 ewes for general studs, taken over the whole of Australia. Tables of the distribution of all sheep according to flock size can be found in most year books published by the State Government Statisticians. Registered and non-registered sheep are included,

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and there is no separation by breeds. Figures for New South Wales (1952/53) and Queensland (1952), the States with the greatest number of Merinos, indicate that 80 per cent. of sheep in New South Wales, and 97 per cent. in Queensland are run on holdings with at least 1,000 sheep per holding, while 59 per cent. in New South Wales, and 92 per cent. in Queensland are on holdings of 2,000 sheep or more. In New South Wales 13 per cent., and in Queensland 36 per cent., of sheep are on holdings running 10,000 or more.

(b) Husbandry

The general husbandry practice might be called "extensive". There is no shepherding of the type common in some countries. Most sheep-lands are now fenced, and the sheep are grazed in the open, in many cases being handled only a few times a year. Stocking rates vary considerably with location, running as low as one sheep to 20 acres or more.

Mating times also vary with location, the rams being put with the ewes for periods of approximately six weeks, in some areas in the spring, in others in the autumn. Mass mating is largely practised, though there is pedigree work in some, but not all, studs. Shearing is usually done annually, at times which vary with location. There may be occasional exceptions, due to circumstances.

(c) Vital Statistics

The average lamb-marking percentage for the industry (i.e., per cent. lambs marked to ewes mated) is of the order of 60, but the variation is very great, both from season to season in the same locality and from locality to locality.

Ewes are seldom mated before they are two-tooths, and in some cases, notably the New England district of New South Wales, they may not be mated until they are four-tooths.

Figures for annual losses among ewes of different ages are difficult to obtain, and vary considerably with season and locality. In some areas they may be well under 5 per cent. for ewes less than eight years of age.

The breeding life of the ewe also varies; flock ewes are cast-for-age at five or six years in parts of South Australia, while in some top studs ewes may be kept as long as they are capable of raising a lamb. In general, however, the casting-age could be said to be six to eight years.

The age-distribution of rams also varies considerably, but in general, rams would not be mated at a younger age than eighteen months.

The generation-interval, all-important for predictions of genetic progress, is of the order of four to five years. For present purposes, it has been taken as four years.

The vital statistics of the industry which are relevant to breeding problems have been summarised and discussed by various authors (Granger, 1944; Turner, 1951 a; C.S.I.R.O., 1952; Moule, 1952).

III. DEFINITION OF "PERFORMANCE"

The Merino breeder is usually concerned with producing the maximum quantity of wool of a specified quality. To maintain flocks and allow for some selection, lamb marking percentages must also be kept as high as possible.

"Quantity" is easily defined in measurable terms. For ewes, **greasy fleece** weight is sufficiently accurate, but for the final selection of top stud rams, it is recommended that a sample of wool should be scoured to get an estimate of **clean** wool weight.

"Quality" is not readily defined in measurable terms. At present wool is sold in Australia after being classed by visual appraisal. According to an analysis by Young and Dunlop (1956), the visually-appraised characteristic which has the greatest influence on price per pound is "spinning count" or "quality number", a classification supposedly on fineness, but in fact based mainly on number of crimps per inch.

At the International Wool Textile Conference held in Australia in 1955, workers in textile research were asked by biological research workers (Turner, 1956 a) for information as to the importance in manufacture of various characteristics of raw wool. The information was required to guide breeders in their selection programmes. It was felt that an analysis of factors influencing price was only a temporary solution, and that more fundamental knowledge was

necessary of the manufacturer's requirements, in measurable terms. Clear answers to the questions were not forthcoming, although some research is in progress. The desirability of uniformity of fibre diameter and length was stressed, but without any specific guidance as to tolerance limits. The information obtained is to be published as a special conference bulletin.

In the absence of specific information concerning measured characteristics, the present system of visual appraisal of quality must be used for the time being, with some check on measurable factors such as length and diameter. A system for definition of performance, partly by visual appraisal, partly by measurement, with fleece weight as a major criterion, was agreed on at a Fleece Measurement Conference held in May, 1954. This conference was called by C.S.I.R.O. and was attended by all workers in the field from various Australian Commonwealth, State, and University organisations. The proceedings (C.S.I.R.O., 1954) are for limited circulation, but the findings have been summarised (C.S.I.R.O., 1955). The question has also been discussed in detail by Morley (1955b). The literature relevant to the use of measurement as an aid to selection has recently been reviewed by Turner (1956b).

Recommendations with an emphasis placed on fleece weight apply to Australian conditions, where wool is the major product from most Merino enterprises. Research is shortly to be undertaken by C.S.I.R.O. to investigate the possibility of combining better mutton qualities with wool in the Merino. If the main products of the industry change, then the definition of performance will have to be modified. The same comment applies to the possible results of research on efficiency of wool production, which may lead to criteria for selecting animals which produce the most wool for the least feed consumption.

One point which must be stressed, however, is that, for maximum genetic progress in any character, the number of characters being considered when defining performance should be kept to a minimum. The problem of selection for more than one character is discussed later.

With the present definition of performance (maximum amount per head of wool of a specified quality, plus maintenance of as high a lamb-marking percentage as possible), a major part of the performance, namely, wool production, can be measured phenotypically on the sire. This situation is in direct contrast to that which obtains with dairy cattle or poultry, and has a considerable influence on the choice of a breeding plan.

IV. SELECTION

Selection may be required at the following stages of a breeding plan:-

- (a) Selection of the strain of sheep to be used in a particular environment, without crossing.
- (b) Selection of breeds, strains or lines for crossing.
- (c) Selection of individual sheep within a flock,
 - (i) For use in the same flock — single characters.
 - (ii) For use in the same flock — more than one character.
 - (iii) For use in different flocks.

(a) Selection of strain

Certain Merino strains have become quite clearly defined, and in choosing one a breeder has to consider not only the type of wool he wants to grow, but also the possibility that one strain or another might be better adapted to his particular environment. In 1948, the C.S.I.R.O. initiated a comparison of five strains (one fine-, three medium-, and one strong-wool) in three widely different environments. Dr. Dunlop, who is in charge of the trial, has made progress analyses of his results (C.S.I.R.O., 1956). The first point of note is that the strains retained distinctive characteristics in all environments. Secondly, Dunlop found strain x environment interactions which were statistically significant but small in magnitude, and for the most part of no great practical importance.

It is of interest to record a problem of possible adaptation of strains which is being investigated in Rajasthan (India), by the Director of Sheep and Wool Improvement, Mr. N. L. Narayan, and his officers. These workers have defined three separate "strains" within the so-called "Bikaneri" breed of carpet-wool sheep, which constitute the main sheep population of Rajasthan. Small flocks of these three "strains" are being maintained and observed at the Sheep Experiment Station at Jaipur, together with different "strains" of other breeds, eight in all. Some interest centres in investigating whether or not these eight types have been developed in response to the demands of different environments.

Rainfall in the sheep-growing areas varies from 5 in. to 40 in., and the vegetation is correspondingly diverse.

(b) Selection for crossing

This problem is not easily separable from its associated mating plan, and will be discussed in the next section.

(c) Selection of individuals within a flock

Sometimes selection is based on only one character, but more often it is on more than one. Many of the problems in the two cases are similar, and it will simplify the discussion to deal with single characters first, dealing later with the complications which arise when several characters are under consideration.

Animals being selected from within one flock may be required for use in the same flock or elsewhere. The problems arising in these two cases are quite different, and will be dealt with separately.

(i) For use in the same flock — Single characters. The main aim in choosing animals is accurate selection of the genotype. This, however, must always be assessed on the phenotype, either of the individual itself or of a group of its relatives. Accuracy of assessment of the phenotype must, therefore, be considered, together with the extent to which the phenotype is an indication of the genotype.

Accuracy of assessment of phenotype: Four main points arise in relation to the assessment of phenotype — the possibility of assessment on both sexes, the actual technique to be used, the number of repeated assessments which are required, and the age (or ages) at which they should be made.

As already noted, Merino breeders are fortunate in that wool, the major item in the performance record, is produced by the ram and can be assessed directly on him. Throughout most of the industry the present method of assessment for both ewes and rams is visual appraisal for general merit. Progeny-testing is carried out in a few instances, but the progeny are usually assessed by visual appraisal.

Observations by Riches and Turner (1955) have shown that replacement of visual appraisal by weighing of individual fleeces would at least treble the selection differential* for lifetime fleece weight, and double the selection differential for money return per head. Morley (1954b) and Moule (1954) have found similar increases in the selection differential for fleece weight.

At present, there is no rapid substitute for visual appraisal of wool quality; this question has already been discussed in greater detail under "Definition of Performance".

One way of increasing the accuracy of an observation is, of course, to repeat it, and to determine the value of repeated measurements on any characteristic its "repeatability"† must be known. Morley (1951b) has found a repeatability of 0.7 for greasy fleece weight — a figure which indicates that selection on one annual fleece weight is sufficient. Riches and Turner (1955) found no advantage in waiting for a second full fleece before selection. They also found selection at seventeen to eighteen months for ewes preferable to selection at six to eight months.

The questions of the earliest possible age of selection for rams and the influence of age on measured characteristics of the ram's fleece are under investigation in C.S.I.R.O. experiments. Some American workers, including Pohle (1942) have tackled the problem of selection at weaning, but as the animals in their experiments were shorn for the first time at twelve months, their results do not contain information on the predictive value of fleece weight at weaning. Russian workers (Sannikov, 1939) have discussed the possibility of assessing animals at weaning, but with no mention of fleece weight.

Phenotype as an indication of genotype: This question is tied up with the type of mating plan, but in view of the decision reached later in this paper

*The amount by which the mean of the selected animals exceeds that of the unselected group from which they came.

†"Repeatability" measures the extent to which an animal's superiority at selection is maintained throughout its life. A repeatability of 0.7 means that an animal with a fleece weight at selection one pound above the mean would have, on the average, a superiority of 0.7 lb. in each succeeding year.

that mass selection should be advocated at present in Australian sheep-breeding, it is appropriate to introduce at this point a comparison of selection on phenotype with selection by assessment of relatives. Lush (1947) carried out a theoretical investigation of the relative efficiency of various ways of combining an individual's performance with that of its relatives, ending with a linear score combining the two. Morley (1951 a and 1952) was the first to attack the problem for the Australian Merino, and concluded that progeny-testing was not worth while when selecting a sire from among a group of rams reared together. In a paper (unpublished, 1954) read before the Australian Genetics Society at Canberra, Turner adapted the formulae developed by Lush (1947) to investigate various ways of using half-sib testing for Merinos, and again concluded that selection on measured phenotype of the individual was the most profitable form when choosing a sire from a group reared together.

The crux of the problem is the "heritability"* level. If the heritability level is high, selection on measured phenotype is the most profitable form of individual selection; if low, then information on relatives will be of value. The classification "high" or "low" cannot, of course, be absolute. In general, if the heritability level is over 0.3, selection on phenotype will supersede methods involving the examination of groups of relatives. For fleece weight and any measured fleece characteristics so far studied in the Merino, the heritability level has been well over 0.3 (Morley, 1951b; Turner, 1954; C.S.I.R.O., 1955).

One advantage of this conclusion is that in a large number of cases pedigrees need not be kept. If a breeder wished to be able to use an outstanding sire extensively, some pedigreeing would, of course, be required so that inbreeding could be estimated and, if necessary, controlled. But for mass selection on phenotype, no pedigrees need be kept. This is an advantage under Australian conditions, in view of the small amount of pedigree work in existence.

It should be stressed that the conclusion about selection on phenotype applies only to animals reared in the same environment. For rams of the same age, a direct comparison can be made. For rams of different ages, their deviations from the grand mean of their own drop must be compared.

The problem of comparing rams grown in different environments is discussed in the section entitled "Selection of individuals — For use in different flocks".

(ii) For use in the same flock — More than one character: The problem of how best to use several characters in selection was first attacked by Smith (1936) and later by Hazel (1943). Their solution was to combine the characters into a single score or "selection index". Hazel and Lush (1942) compared three methods, and found the linear score to be most efficient. The other two methods are "independent culling levels" (where a breeder fixes a certain level for each characteristic and culls all animals which fall below in any characteristic), and "tandem selection" (where the breeder concentrates on raising one characteristic at a time, ignoring the others meanwhile).

Although selection indexes are theoretically most efficient and, therefore, of value in research, there are difficulties about their use in commercial practice. Their calculation depends on the estimation of genetic variances and covariances. If these were relatively constant from flock to flock, a standard set of weighting coefficients could be computed and widely used. In fact, they have not been found to be constant, nor is there any reason why they should be. Each flock must have its own set of coefficients calculated. Even if, eventually, large properties in Australia employ their own geneticists, as is done in some animal industries in U.S.A., there remains the problem that estimates of genetic correlations have a high error until large quantities of data have been collected. This objection should not deter research workers, but it is important in commercial application.

The system of "independent culling levels" appears to offer greater scope for wide commercial use, provided the number of characters is kept small. The system recommended by the Fleece Measurement Conference (C.S.I.R.O., 1954 and 1955) involves a preliminary selection for "off-type" fleeces, which amounts to fixing a culling level for quality. This culling rate should be as low as possible. Final selection is then on fleece weight. As shown by Hazel and Lush (1942) the loss in efficiency for independent culling levels, compared with the selection index, is not great when the proportion saved is small, as it is with rams. With 1 per cent. of animals saved, the ratio of genetic gain, using a selection index, to genetic gain, using independent culling levels, is 1.10 for two

*"Heritability" measures the proportion of the parents' superiority which will, on the average, appear in their offspring.

characteristics or 1.25 for five. These figures apply only to uncorrelated characters; the equations for more complex cases remain unsolved.

In addition to wool production, maintenance of a high lamb-marking percentage was included in the definition of performance. At present there is no way of determining a ewe's potential as a breeder except by mating her and observing the results. The possible exception to this statement is Terrill's observation (1949) that face-cover is negatively correlated with fertility in his Rambouillet flock, an observation which has been repeated in N.Z. on the Romney (Rae, A. L., and Clark, E. A., personal communications, 1955) and in Australia on the Merino (Fail and Dun, 1956). No high degree of correlation has been found, however, in C.S.I.R.O.'s Merino breeding flock at Gilruth Plains, Cunnamulla, which has a much lower degree of face-cover than Terrill's flock.

Observations are being made by C.S.I.R.O. on the repeatability of lamb-bearing and rearing, and the possibility of using the early years of a ewe's record as an indication of her breeding performance. Further investigations are being made of the heritability of the two aspects of fertility. The evidence so far (Barrett, 1956) indicates that no great improvement in lamb-raising can be expected from culling on a ewe's early records. If any culling is to be done, however, the recommendation is again that the method of independent culling levels should be used — namely, that ewes be selected as two-tooths on wool production, with a culling margin left for subsequent selection on reproductive performance, if required.

-This recommendation arises partly from the overwhelming importance of wool in the flock economy. If mutton were to increase in importance and to become of equal or greater importance than wool, as it is in U.S.A., it would become necessary to reconsider the recommendations for selection.

(iii) For use in different flocks — One or more characters: Selection of individual animals (e.g., rams) from outside a flock involves two additional problems besides those discussed in the preceding paragraph.

Comparison of phenotypes grown in different environments: If the introduced rams are to be compared with home-grown rams, or with rams from a different source, direct comparison of the phenotypes will give no indication of the genotypes. Comparison of rams from two sources at a show or a sale-ring, for example, is of no value as an indication of their worth for genetic improvement. If the mean fleece weights for unclassified rams of the same age on their home properties were known for a period of years, so as to give an accurate base for each property, then the rams could be compared in terms of deviations from the appropriate base. Under existing conditions this information is not likely to be available. There is no certainty at present that it would be conclusive, and further information is required on gene x environment interactions.

Performance-testing under standard conditions has been tried for other live-stock overseas notably dairy cattle and pigs in Denmark. The actual running of the standard conditions for the dairy cattle is presenting some problems, and A. Robertson (personal communication, 1955) has found greater differences between progeny groups under standard conditions than in the field. Performance-testing for rams could be organised much more simply, as the rams themselves, and not their progeny, could be kept under standard conditions for a given period of time. Before performance-testing on a centralised basis can be advocated, however, answers are required to some of the gene x environment questions raised in the next section.

Under existing conditions, progeny-testing appears at first sight to be one way of comparing rams grown in different environments, but there seems to be no experimental work nor theoretical consideration of the comparative efficiency of various methods.

Gene x environment interactions: Dunlop's observations on the strain trial, previously discussed, indicated a lack of strain x environment interactions of any practical importance. However, the question of the possible existence of gene x environment interactions for individual animals remains unanswered. It is one of considerable importance for the whole of the Australian Merino industry, in view of the large concentration of the major studs in the better environments. Will a ram which ranks high among his fellows in one area also give superior progeny to theirs when used in another area? If Dunlop's results with the strains held for individuals, the answer would be "yes", as the strains ranked in the same order in all environments. But there were significant variations in the actual differences between strains, and the great magnitude of these differences might have made it difficult for the variations actually to change the

ranking. Differences between individual rams would not be as great as the strain differences, and the possibility remains that gene x environment interactions might be important. Plans are being made to investigate the point, with Merinos, in C.S.I.R.O.

Falconer and Latzewski (1952) carried out selection experiments with mice to throw light on this point. They selected for large body size under two planes of nutrition (**ad lib.** and 75 per cent. of normal) and obtained response in both lines, though it was less on the restricted than the full diet. At three points (after 5, 7 and 8 generations of selection) portions of each line were reversed in diet. The mice selected on the poor diet showed growth rates on the **ad lib.** ration comparable to those of the mice which had been selected on it. But the mice selected on the high diet fell far below the mice selected on the poor diet when transferred to the latter. To quote the authors' own summary, "Thus, improvement of the genotype for rapid growth on a high plane of nutrition carried with it no improvement for growth on a low plane. But improvement of the genotype for growth on a low plane did carry with it a considerable improvement for growth on a high plane". The authors point out that the physiological responses to selection which have led to these results present "a complex problem which cannot yet be solved". They considered that they had probably been selecting, in effect, for different characters in the two lines, although bodyweight was the selection criterion in each case. This point also requires to be investigated with sheep — namely, do the characteristics required for survival and high production in one environment differ from those in another?

V. MATING PLANS

Before starting a discussion of mating plans, it is necessary to review very briefly some ideas on the cause of genetic variability, as these causes may influence the choice of plan.

The total phenotypic variation of a characteristic within a flock may be considered as coming from two sources — genetic and environmental. The genetic variability itself may come from three direct sources, with possibly two types of gene x environment interaction as well:

1. Additive genetic variance, which is assumed to depend directly on the number of "plus" genes for the characteristic which are present.
2. Interaction between genes at the same locus. This may express itself as: **Dominance**, the heterozygote at any one locus having a value up to, but not greater than, the higher homozygote, or **Over-Dominance**, the heterozygote at one locus then having a value greater than the higher homozygote.
3. Interaction between genes not at the same locus, which is known as "epistasis".
4. Unconscious gene x environment interactions of the kind already discussed, when animals within the flock somehow find better environments for themselves, although the whole flock is run together.
5. Conscious gene x environment interactions, when the better animals are picked out by the breeder and given preferential feeding.

Gene x environment interactions are not likely to be important in influencing the decision for any breeding plan **within** a sheep flock. Those mentioned under 4 cannot be estimated, while those under 5 can be avoided.

The relative magnitude of the other fractions of the genetic variance govern the initial decisions regarding a mating plan. If the additive genetic portion (which is the portion expressed in the "heritability" figure) is large for any characteristic, that characteristic should respond to selection. There have been cases recorded in laboratory experiments, however (e.g., Reeve and Robertson, 1953), where, after long continued selection, the heritability has been still high although response to selection had ceased. In general, however, if there is high heritability, the simple method of mass selection should be profitable — that is, the method of merely selecting the best animals from each generation, and putting them into the breeding flock. With a high heritability, as we have pointed out, selection on phenotype is adequate. If, or when, these simple methods fail, other methods are available for plants and some types of livestock; whether they will be valuable with sheep has not been shown. Some of these methods involve exploitation of hybrid vigour, and the choice of plan involves deciding whether "dominance" or "over-dominance" is the most likely contributor to intra-allelic interaction. A considerable controversy on this issue

still rages in some genetic circles, and some interesting fields of research are devoted to developing techniques for separating the non-additive portions of the genetic variance.

In the following sections it is proposed to discuss mass selection, to review briefly some of the other breeding plans which are used for cases where mass selection is not effective, and to give reasons for thinking that mass selection is likely to be the optimum mating plan for Australian conditions for some time to come.

(a) Mass Selection

Two questions arise immediately when mass selection is discussed. Firstly, for how long is any response to mass selection likely to continue? Secondly, under long-continued pressure on one characteristic, is there likely to be any deleterious effect on another, particularly one (or more) which might affect the well-being of the animal?

(i) Response to selection: Because of the long generation interval in most livestock, selection experiments covering a number of generations are difficult to organise and are few in number. There have been many laboratory experiments for selection in quantitative characters, however, particularly with mice and *Drosophila*. Some results of the well-known experiments with mice are summarised in Table 1.

These results all show a great response to selection at first. There appears to be no slackening of response up to the 9th generation. In later generations the pattern varies; there may or may not be a plateau and in some cases there has been continued response for as long as 23 generations. Both Goodale and MacArthur struck trouble with sterility, but Falconer and Falconer and King did not, though some lines did show decreased litter size.

Falconer and King consider that each of the strains which they crossed (the Goodale and MacArthur strains) had reached a "plateau", and discuss the reasons for reaching selection limits. In their material, they consider loss of genetic variance more likely than the attainment of a physiological limit or opposing natural selection (i.e., loss of fitness). Lerner (1954) in summarising the results of selection experiments, suggested the possibility that existing systems were in balance, and that any extreme selection pressure would upset the balance and reduce fitness.

A main point of interest to animal breeders is how far selection can carry a character before a limit is reached. In the examples quoted in Table 1, selection for large body size had produced increases as high as 73 per cent. (Goodale, 50th generation) and 71 per cent. (MacArthur, 21st generation). The initial mice had not been subjected to any selection at all. Goodale does not quote a heritability figure, but MacArthur states that heritability with his mice fell from 25 per cent. initially to 10 per cent. at his 21st generation.

In the Australian wool industry, we are dealing with an animal to which selection has been applied for many years. It is very difficult to tell how much progress has been achieved through selection, because improved husbandry has been allied with it. The average wool cut for Australian sheep in the 1880's is quoted by Dalgety and Company Limited (1951) as 5 lb. per head, whereas since 1930 the average has fluctuated between 8 and 9 lb. In the absence of any breed separation or any indication of environmental changes, these figures are very crude, but they indicate the sort of change which has taken place. This change is of the same order as the ones already mentioned for the laboratory mice — an increase of 70 per cent. There is a suggestion of a plateau in the wool cuts since 1930, i.e., after about 12 generations, counting a sheep generation as four years.

There are reasons, however, for considering that wool production will respond further to selection.

Heritability: MacArthur quotes a figure of 10 per cent. for heritability of bodyweight at his 21st generation, at a point where response was slackening. Estimates for the heritability of fleece weight in the Australian Merino, computed by Morley (1951 b, 1955 a), Turner (1951 b and further unpublished data), and Shinckel (unpublished) are all over 30 per cent. and range as high as 50 per cent.

Response obtained already with sheep: Goodale considered he was still obtaining a response to selection at his 50th generation, although Falconer and

TABLE 1
SUMMARY OF RESULTS OF SOME SELECTION EXPERIMENTS WITH MICE

Author	Character under Selection	Method of Selection	Generations of Selection	Starting Value (Males-g)	End Value (Males-g)	Changes in Rate	Correlated Responses in Characters for Fitness	Asymmetry
Goodale (1938)	Large body size (60-day weight)	Progeny test	12-16	26.3	36.5	No slackening.	None reported by Goodale. MacArthur mentions sterility. Trouble with sterility.	—
	Large body size (60-day weight)	Progeny test	Continuation of breeding experiment up to 50th generation.	26.3	45.7	Selection had to be relaxed 1944-47 to permit build up because of trouble with sterility. Now increasing again.		—
MacArthur (1949)	Large (L) and small (S) body size (60-day weight)	Full-sib test plus phenotype size (60-day weight) also some successful pairs remated	21	23.2	L—39.8 S—12.0	Rate slackening, but still progress.	Litter size changed in same direction as body size. Mentions sterility, but does not say which line.	Large changed at faster rate.
Falconer (1953)	Large and small body size (6-week weight)	Phenotype within litters	11	21.6	L—25.2 S—14.4	No slackening.	Litter size increased at first with body size then returned. Decreased continually with small.	Small changed at faster rate.
Falconer and King (1953)	Large and small body size (6-week weight)	Phenotype within litters	9	29.5	L—32.0 S—25.0	No slackening.	Slow decline in litter size in both lines.	Small changed at faster rate.

King failed to obtain any response when they used his mice. MacArthur's successor found no response after the 21st generation, whereas Falconer and King did get a response with some of his mice. The question of further response in these mice seems an open one. What is important, from the sheep-raising viewpoint, is that selection for fleece-weight **has** produced a response, even after many years of selection. Probably selection has not been sufficiently closely directed towards the fleece itself for additive genetic variation to be exhausted — breeders have always had a number of other points in mind as well.

Selection experiments directed solely towards fleece weight, other characteristics being ignored completely, were initiated in 1954 by C.S.I.R.O. at the National Field Station, Gilruth Plains, with medium-wool Peppins. There are two lines, one for high, one for low clean wool weight. The first results became available when ram progeny were shorn in August, 1955, when they were 10-11 months old and were carrying 146 days' growth of wool. The mean clean wool weight of the control, unselected group was 3.1 lb., that of the high fleece weight group 3.5 lb. and of the low 2.8 lb. The response to selection in each direction is thus approximately 10 per cent. of the control group mean. In other selection experiments in C.S.I.R.O., commenced in 1950, two methods of selection of sires are being compared — selection on measured phenotype and selection on measured half-sib performance plus phenotype. In these groups selection is on clean wool weight with some attention to quality. Two-tooth ewe progeny in the selected groups at the 1956 shearing cut 6 per cent. more clean wool per head than the controls.

Selection has thus produced an immediate response in fleece weight in both experiments. The experiments are planned to continue for many years, to find out how long the response continues in subsequent generations.

Morley (1955 a), working with medium-wool Merinos, has also obtained instant response to up-and-down selection for fleece weight; Neale (personal communication, 1955), working with grade Rambouillets for ten years in the field in New Mexico, has obtained responses to selection for high fleece weight, as have Burns and his associates in Wyoming (Johnston, A., personal communication, 1955). Euston Young, working with Merinos at "Noondoo", Queensland, raised the mean fleece weight in his stud by 2 lb. in 20 years after he introduced selection on measurement. There was some improvement of management as well, but on the heritability estimates found a large proportion of the gain could have been genetic.

Investigations in progress cover not only clean wool weight but associated characteristics. The C.S.I.R.O. high-and-low selection lines cover eight characteristics. Three pairs of groups (selection for body size, staple length and fibre number) have been established for some years, but are not much beyond the first generation. The other five pairs with selection for fibre diameter, wrinkle score, clean wool weight, clean wool weight per unit skin area and per cent. clean yield were established in 1954.

Estimates of heritability obtained in the main body of the experiment have been high (over 30 per cent.) for all characteristics, and there has also been a marked response in all the high-and-low selection groups. With the exception of clean-scoured yield and wool weight per unit skin area, where the differences between the high-and-low group progeny are respectively 13 per cent. and 14 per cent. of the control group, all other differences between high-and-low groups exceed 20 per cent. of the control, and run as high as 32 per cent. for staple length.

(ii) Undesirable correlated responses: The possibility of undesirable correlated responses, particularly in factors associated with reproduction, must be investigated. In the C.S.I.R.O. high-and-low selection groups which have been established for some years, and in which selection is for a single character, lamb losses in the first few days of life were heavier in some years in the progeny of half-sib matings of maiden ewes than in the progeny of unrelated matings of maiden ewes in other groups. The progeny of the half-sib matings had a higher generation number as well as a higher coefficient of inbreeding.

Mortalities in the main selection groups have been no higher than in the control group. In these groups selection has been on fleece weight with some attention to quality, but there has been a small amount of culling of ewes for failure to produce or rear lambs.

Workers in New Zealand (Rae and Clark, personal communications, 1955) have reported a negative genetic correlation between fleece weight and fertility,

which appears to operate through face-cover. Terrill (1949) found a negative phenotypic correlation between face-cover and fertility. Analyses of the Gilruth Plains data have shown a regression of fertility on face-cover so slight as to be of no practical importance. A much lower mean score for face-cover in this flock may be the reason for the difference. An analysis of the genetic correlation between fleece weight and fertility is in progress. This analysis is not complete, but no significant trend has been found. Preliminary analyses by E. Roberts (personal communication, 1955) of some of Dunlop's Strain Trial data, with reproduction records on five strains of sheep, again indicate no association of any magnitude. Further analyses of both sets of data are in progress.

Before passing to a discussion of other mating plans, some reference might be made to mass selection with other organisms. Goodale (1937) quotes Payne (1918) as having raised bristle number in *Drosophila melanogaster* from 4 to 9 in 30 generations, with little change thereafter. Of the initial population in this case 99.5 per cent. had only 4 bristles, and selection began from a single pair, one of which had 4 bristles and one 5. Woodworth, Leng and Jugenheimer (1952) have reported on the famous Illinois corn experiment, with selection for high and low oil content, and high and low protein content, for 50 generations. In the high-oil line the oil content rose from 4.7 per cent. to 15.4 per cent., with no sign of slackening, while in the low-oil line the content fell to 1.0 per cent. by about the 30th generation, with little subsequent progress. The protein content in the high-protein line rose from 10.9 per cent. to about 19.0 per cent. by the 35th generation with little subsequent change, while in the low-protein line it fell steadily to 4.9 per cent. with no sign of slackening. Two generations of reverse selection produced changes in all except the low-oil line. Manning (1955) reported continued response to selection for yield in cotton, although the foundation stock was a single plant.

(b) Other mating plans

In the last section, successful responses to selection were reviewed. Early this century it was considered in certain experiments in U.S.A. that corn was failing to respond to selection for yield, and the technique of crossing inbred lines was developed, beginning with the work of Shull and of East in the period 1908-1910. (For a review of this early work see Shull (1952) and Hayes (1952)). The spectacular success of this work led to its adaptation to other organisms, though more recently some workers have queried whether it might not be possible still to obtain considerable advance with straight selection even in corn.

In the meantime, line-crossing has been developed and widely used commercially for pigs and poultry, as well as for various plants. Much research has been directed towards developing techniques for testing crosses, and this has involved theoretical consideration of the mechanism behind the phenomenon of "heterosis" or "hybrid vigour" — i.e., the superiority of a cross between two lines (or strains or breeds) over the parents. As mentioned earlier, there are two main schools of thought, one attributing hybrid vigour to "dominance", the other to "over-dominance", though neither would rule out the possibility of contributions from epistasis.

The basic principle behind either hypothesis is that, when characteristics are controlled by a large number of gene pairs, a cross between two lines is likely to contain more heterozygous gene pairs than either of the parents. The "dominance" hypothesis then draws on the frequently-observed correlation between dominance and beneficial effect to postulate that, if one allele is dominant to the other, some at least of the loci which were homozygous for the deleterious recessive in either parent will be heterozygous in the hybrid, and the deleterious genes will be masked by their dominant beneficial alleles. The "over-dominance" hypothesis, on the other hand, postulates that there is something about heterozygosity *per se* which is stimulating.

There is extensive literature now on the problem of estimating the fractions of genetic variance attributable to various sources, and on the development of crossing techniques which will exploit these various fractions. Papers by Hull (1945), Comstock, Robinson and Harvey (1949), Crow (1952), Hayman (1955), give discussions of the problem, and bibliographies for this field of research.

The success achieved with these techniques in some organisms leads to consideration of their application to others. Should they be considered for application in Australian sheep-breeding?

The first requisite for achieving hybrid vigour is that the lines being crossed should be genetically dissimilar — that is, they should have been closed to each other for some time before crossing. With quick-breeding animals like poultry and pigs, this genetic isolation can be achieved much more readily than with sheep. Further, a grower's existing stock can be replaced much more rapidly.

The 24 "parent" studs of the Australian Merino industry and 258 of the studs dependent on them have been closed, and have developed distinctive sheep strains. But according to the estimates of Short and Carter (1955) only 25 per cent. of annual ram replacements for commercial flocks come from these closed studs. Further, as mentioned earlier, there is no information as to the number of commercial flocks which have kept up genetic isolation by drawing their rams consistently from the same stud. Any information which exists indicates that the number is likely to be small. Riches (1953), in a survey of the Merino industry in the eastern half of Australia, set out initially with the idea of tracing the behaviour in different environments of stock derived from the various parent studs. He found it impossible to locate sufficient properties which had been consistent in their source of ram supply. The studs themselves might gain some increase in production by crossing, but this would not pass down through the commercial flocks if those are indiscriminately heterozygous already.

In this connection, it is of interest to consider the time which would be required to replace one sheep type by another in a breeding flock. Even if we assume that one-quarter of the ewes is replaced annually, and that rams of the new type are used continually, it will be 11 years before all the flock has at least $\frac{3}{4}$, and 16 years before all the flock has at least $\frac{7}{8}$, of the new "blood".

Crossing of existing strains, therefore, does not seem to offer great promise for exploiting hybrid vigour in increasing Australian Merino wool production. Development of new closed lines is most quickly achieved by inbreeding, but the low incidence of twins makes this process with sheep again much slower than it is with pigs or poultry. Terrill, working at the Western Sheep-breeding Laboratory of the U.S.D.A. at Dubois, Idaho, has been carrying on work initiated in the early days of the station, designed to develop inbred lines with sheep and test their crosses. In 1948 Terrill initiated a non-inbred group with selection on an index for general merit, and up to the present (as stated by himself in an address to the Australian Society of Animal Production in 1955) has found straight selection to give greater progress than the crossing of inbred lines. Whether straight selection will eventually fail and leave the superiority with line-crossing remains an open question. Terrill and his group are collaborating with workers from other experiment stations in the production of a large number of inbred lines, each containing a small number of individuals. This system is planned to test as many line-crosses as possible.

One other overseas experiment might be mentioned in this connection. The Animal Breeding Research Organisation in Edinburgh is planning a diallele cross involving several breeds with the object of partitioning the genetic variance. This experiment should yield evidence on the extent of heterosis with sheep and the characteristics affected. It will be of particular interest in Australia in view of the fact that recently-imported Australian Merinos are to be included.

In Australia, research is proceeding in a different direction. The components of fleece weight — body size, wrinkling score, staple length, fibre diameter and fibre number — and their relationships are being studied, and, as has been mentioned, selection for each is in progress. This selection has already demonstrated not only that each component is highly heritable, but also that there are no strong genetic correlations between some of them, so that it might be possible to re-assemble them in different ways to raise production, while still producing wool of a specified quality. If the measured fleece characteristics of established lines were known, the introduction of rams designed to raise the level of a specific fleece component might be a profitable way of increasing production, even without previous genetic isolation of the new type from the existing flock. The method has not yet been tried quantitatively, but it is in essence the time-honoured method of animal-breeders, put on a quantitative basis.

(c) Prediction of Progress

The foregoing discussion has led to the conclusion that mass selection on measured phenotype is likely to give greatest progress for raising Australian Merino wool production. The actual amount of progress will depend on factors

such a flock size, lamb-marking percentage, rate of ewe replacement, per cent. rams used and rate of ram replacement. However, one plan can be given as an example (C.S.I.R.O., 1955):

Assume a flock of 2,000 breeding ewes, with a lamb-making percentage of 75. The ewes are mated five times and the annual culling rate is 30 per cent. Suppose the breeder closes his flock and selects the best 300 ewes as a ram-breeding nucleus. If he mates 2 per cent. of rams with his ewes, and uses each ram for two years he can expect an annual genetic gain of approximately 2 per cent. in fleece weight if he uses preliminary eye appraisal for wool quality and bases his final selection on fleece weight.

These gains will be achieved most quickly for the whole industry if quantitative methods are adopted in the "parent" studs. However, in the absence of information about the genetic superiority of these studs and about gene x environment interactions, there is much to be said for the introduction of quantitative methods at all levels of the industry. Selection of even flock ewes on fleece weight instead of by eye appraisal, for example, can add 2 per cent. to the **current** production of a flock, though the main **genetic** gain comes from the higher culling rate which is possible in ram selection.

Reference has already been made to the fact that 59 per cent. of New South Wales sheep and 92 per cent. of Queensland sheep run in flocks of 2,000 or more, and the average size of the parent studs is well above this. The general size of a breeding unit is, therefore, sufficiently large to gain considerable benefit from mass selection.

One of the risks of closing a small breeding unit, of course, arises from the dangers of inbreeding. On this point, again, further information is required with sheep, particularly over a range of strains. Morley (1954 a) with the Australian Merino, and Hazel and Terrill (1945, 1946 a and b) with the American Rambouillet, have already published estimates of the regression of fleece characteristics on degree of inbreeding, but further figures on a wider range of material are desirable. Answers to questions such as "How much should an outstanding sire be used?" depend on balancing the sire's superiority against the amount of depression to be expected with advancing degrees of inbreeding.

How far we can go with mass selection is something which we can only determine by trying. But a glance at the wide diversity of animal types — from Shetlands to Shires, from Dachshunds to Great Danes, from Tasmanian to South Australian Merinos — is sufficient to show us the power of selection as a tool. And anyone who might think that these achievements are accomplished and mark the end of change has only to examine the results of recent selection experiments with sheep to see that the age of response is not over.

VI. CONCLUSIONS

1. "Performance" for the Australian Merino is defined as production of wool of a specified quality, plus maintenance of as high a lamb-marking percentage as possible. "Quality" is at present assessed visually, but when textile research leads to information on characteristics important to manufacture, it may be possible to replace visual appraisal by measurement.
2. Selection problems can be discussed separately from mating plans, and fall into three sections — selection of strains, of lines within a strain to be used for crossing, and of individuals within a flock.
3. In a C.S.I.R.O. trial just concluding, five major sheep strains were run in three environments. Strain x environment interactions, though statistically significant, were in general small in magnitude and of no practical importance.
4. Strain or line-crossing is not considered likely to be of great benefit to the wool-growing industry as a whole, at least under present conditions.
5. For selecting individuals from among a group raised together, the use of independent culling levels is recommended under existing conditions in the industry, rather than a selection index. Preliminary appraisal on wool quality, followed by selection on fleece weight, is suggested. In the case of ewes, it might be necessary to leave a margin for later culling on breeding performance. This recommendation stems from the overwhelming importance of wool in the present flock economy, and will require reconsideration if economic weightings change.

6. There is need for further research (a) on the best method of comparing rams grown in different environments, and (b) on the existence of gene x environment interactions for individual sheep. These points have a bearing on the distribution of rams from central studs.
7. Mating plans can be discussed under the headings of "mass selection" and "other plans".
8. Mass selection on measurement is recommended for the Australian Merino industry. Prospects of advance are bright because:
 - (i) High estimates of heritability have been found for Merino fleece weight and for all measured characteristics associated with wool production which have been studied.
 - (ii) In C.S.I.R.O. experiments with medium-wool Merinos, first-generation results indicate immediate response to selection for clean wool weight and seven other characteristics studied. In the first generation, the smallest difference between high-and-low selection lines was 13 per cent. and the greatest 32 per cent.
9. Preliminary analyses indicate no strong **negative** correlation between fleece weight and fertility in the Australian Merino. Indications of such a correlation have been found with the Romney Marsh breed in New Zealand.
10. The exploitation of heterosis in other types of livestock is briefly discussed, and the suggestion made that these methods are not likely to be of great benefit to the Merino industry in Australia because:
 - (i) Although studs exist which are genetically distinct, there is no evidence of the existence of genetically isolated groups within the commercial flocks, such as could benefit from inter-crossing.
 - (ii) Replacement of existing flocks with sheep from genetically isolated strains would be slow.
 - (iii) Development of inbred lines would be slow and costly, because of the low lamb-marking percentages and the low incidence of twins.
 - (iv) The benefit of such crossing has in any case not yet been demonstrated with sheep.
11. The possibility of increasing wool production by re-combination of components is suggested.
12. Predictions of progress under mass selection can be given. Progress depends on a number of factors, but under one set of conditions which is described, a genetic advance of 2 per cent. per annum in fleece weight is predicted.
13. To make optimum use of mass selection in closed flocks, further estimates of inbreeding depression are required.

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