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in the case of pigs with which Clare's paper dealt, the condition appeared to be dominant in character, and this extremely interesting genetic situation should be followed up further.

Reply: No attempt has been made to draw conclusions on the scanty information at present available as to the mode of inheritance of the condition in pigs. The evidence of South African workers definitely indicates that in their herds of cattle it was a recessive factor. Further information is being sought on the breeding of the boars and the sows referred to in the paper. It would be noted that the boars were Tamworths and the sow part Tamworth, and a common ancestry is possible. Members are requested to report any occurrence of pigmented bones, and if possible to send in samples to the Laboratory.

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THE INHERITANCE OF MULTIFACTOR CHARACTERS IN THE SHEEP

by

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INTRODUCTION:

The elementary idea of propagating superior individuals in the belief that their offspring will likewise be superior has much to commend it. Practical breeders have worked on this principal from the earliest times, and eighty years ago, Darwin built around it a theory which revolutionised biological and social thought. Only comparatively recently, however, have the actual workings of selection been closely investigated in farm livestock. Manifold differences between breeds and strains make it evident that heredity plays a part in determining the grade of economic characters; but orthodox ideas have been profoundly modified during the last ten to fifteen years. At Cambridge, for example, Hammond and his school have demonstrated the most far reaching modifications in economic characters by imposing extremes of environment, while even with stock kept under commercial conditions Lush and his co-workers have found that features affecting production are often only weakly passed from parent to offspring. It is becoming more and more evident that the greatest technical problem facing breeders of farm livestock is that of recognising hereditary potentialities beneath obscuring effects of environment. For a reasonable rate of progress to be maintained in both pedigree and grade animals, something more than simple selection is essential. If rational use is to be made of pedigree details, records of family performance, progeny tests, and inbreeding, however, we must know the relative importance of heredity and environment with some approach to accuracy. When, as in sheep, economic returns come from several almost independent features, the problem becomes more complex, for not all of these are influenced by environment to the same extent. On the final solution of this problem will depend the most efficient methods of selection and culling, the best use of different measures of excellence, and the system of mating leading most rapidly to better stock.

The present project was commenced in 1939, in conjunction with other workers at Massey Agricultural College, to determine the relative importance of hereditary and environmental influences on the main economic characters in a stud Romney flock kept under normal commercial environment. In the course of the investigation it became clear that the amount of selection normally possible, especially among female stock, could produce no appreciable improvement in the hereditary make up of the flock, except over a long period of time (McMahon 1940). In contrast, attention was attracted by the magnitude and significance of variation among the progenies of different sires, and to the possibility of relatively rapid improvement through exploitation of the progeny test. Finally, in collaboration with Dr F.W. Dry and Mr R. Waters, a system of mating was evolved, based on Hagedoorn's (1939) nucleus principle, which it was felt made the most efficient use of all the different sorts of information available (McMahon 1941).

Full description, analyses and discussion of work carried out in 1939 and 1940 would cause trouble with both our Chairman and the Paper Controller; the description would be boring, the analyses statistical and the discussion over-long. The present paper gives only principal results and conclusions in simple terms and a full report is being published elsewhere.

RESULTS:

1. Repeatability of Subjective Gradings:

With the exception of Fleece Weight, none of the characters affecting economic returns from sheep can be measured satisfactorily on the live sheep using objective methods. Personal judgments are the only means of investigation yet available for such characters as Breed Type, desirability of Head Shape, Fleshing, and Wool Character (McMahon 1941). This sort of approach may not be satisfying to the scientist, but it is the one used by breeders, and conclusions derived from such gradings can be applied immediately to sheep husbandry practice. It was clear, however, that errors in grading were likely to account for a large portion of the non-hereditary variance and check tests were carried out over all the features studied.

Table 1. summarises the results in terms of error in judgment and fractions of variance accounted for by the consistency of repeat gradings. Statistically, the latter are correlations, but the non-statistician may multiply by 100 and think of them as percentages of efficiency. If judgment were perfect the efficiency figure would be 100. If, on the average, animals graded high (or low) were really only half as good (or bad) as a single judgment made them out to be, the percentage would be 50. Similarly, other animals would be graded at only half their real value. The "error of judgment" term sets the limits of deviations from the true value of the animal which the judge would not exceed more than once in three times. Only about once in 20 times would the judge's estimate deviate from the true value by as much as twice this figure.

TABLE 1.

Feature Studied	Number of Comparisons	Error of Judgment	Consistency
Head Grading	126	±.51 grade	.474
Breed Type	120	±.52 "	.324
Fleshing	118	±.54 "	.426
Wool Character	558	±.59 "	.540
Count	558	±.48 "	.518

Although the judge seldom errs by as much as one grade, it is clear from the relatively low levels of consistency that the sort of method which we have at our disposal when dealing with many live sheep at a time leaves much to be desired. This is true even when, as in the present case, each sheep is viewed individually. In dealing with rams, however, and in small studs where each sheep becomes known to the shepherd, better accuracy would be achieved. Nevertheless, it is difficult to see how the situation can be improved very much in a large stud or among grade sheep, and it seems safe to conclude that the average sheepman, when culling, can utilise less than half the scope for selection which actually exists in his flock.

2. Genetic Fractions of the Total Variance:

The ratio of variance due to genetic causes, to the total variance in the population is of particular importance because it determines the rate of change under any given system of selection or breeding. Upon this ratio will depend the proportion of the superiority of individuals, selected because they are better than average, which comes to expression in the next generation. For simplicity, the ratio of genetic to total variance may be regarded as a measure of the intensity of inheritance, although this simplified mode of expression cannot be applied if either genetic or environmental conditions differ greatly from those ruling in the data analysed.

The ratio of genetic variance to total variance can be determined in various ways (Lush 1939), and in the present study estimates were derived from:

(1) Correlation coefficients measuring the average similarity between productions in different seasons on the same animal.

(2) Correlation coefficients measuring the average degree of similarity of offspring by the same ram. Since paternal half-sibs have only one quarter of their genes in common, on the average, the correlation must be multiplied by 4.

(3) Correlation coefficients measuring the average likeness within sire groups of offspring to their dams. Where the dams are a selected group, as in the present flock, the regression coefficient must be used instead of the correlation. Since dam and offspring have half their genes in common, on the average, the correlation or regression must be multiplied by 2.

No one of these methods can give a complete picture. Method (1) includes with genetic causes any permanent effects of early environment which persist throughout life. In the present data, too, it is likely to give high estimates because figures for only two years were available for analysis. Ratios derived in this way, therefore, must be regarded as maximum values. Method (2), on the other hand, must give low results if the sires used have been highly selected for uniformity, especially when hereditary effects are strong; if the hereditary effects are weak, the estimates are easily disturbed by environmental effects common to progeny of one sire, but not general in the flock. Examples of such influences would be the use of certain rams early or late in the breeding season, or the preferential treatment of rams sired by special rams. These effects should be small in the present data. As in method (1) range of environment is limited to one year because measurements and gradings on progeny groups were available for the hogget stage only. Method (3) probably gives the most useful alround estimates - if only because it is such a direct measure of the effects of selection. It does not, however, include all the effects of dominance, and along with method (2) must be corrected for inbreeding.

Table 2. records the results obtained in the present study, after correcting for number of common genes (see before).

TABLE 2.

Feature Studied	From Similarity of:						Most probable Value.
	Same Sheep in two different Seasons		Paternal Half-sibs		Offspring and Dam		
	Number studied	Esti-mate	Number studied	Esti-mate	Number studied	Esti-mate	
(From the Voss Flock)							
Head Grading	203	.258	1751	.052	817	.256	.25-.30
Breed Type	203	.238	1651	.187	777	.140	.15
Fleshing	200	.164	1627	.152	748	.122	.13
Wool Character	230	.315	1772	.180	1062	.124	.14
Count	222	.499	1774	.184	1078	.328	.35-.40
Fleece Weight	188	.461	1733	.264	895	.040	*.10-.15
(From the Matthews Flock)							
Wool Character			571	.104			
Count			573	.056			
Fleece Weight			546	.394			

*The value for Fleece Weight inheritance obtained from the offspring-dam regression is unduly low because the dams considered showed a wider range of age and previous physiological history than would be likely to be encountered among grade sheep. The only correction made was for barrenness in the season during which the fleece weighed was being grown. Such a low regression, too, is subject to relatively high sampling errors despite the large number of pairs on which the estimate is based.

The agreement between the results from methods (2) and (3) shown in the table is good for Breed Type, Fleshing and Wool Character. For the strongly inherited features of Head Grading and Count (fibre fineness), estimates from paternal half-sib similarity are low, because before all else, the sires would certainly be carefully chosen for these characters.

It is evident that here, selection of sires is a powerful tool in the hands of the breeder. For these features, too, where inheritance appears to be relatively strong, selection among pedigree sheep must surely rapidly reach a stage where it is concerned more with variability than with average values. This is clearly the case with count, where the breeder must aim at an optimum which will depend upon his environmental conditions (McMahon 1942). Variability, however, will be reduced at a rate proportional to the squares of the ratios of genetic variance to total variance. These would be about .06 and .15 for Head Grading and Count respectively, so that to secure lines of sheep of similar appearance, and with little variation in wool fineness, it is clear that after a few generations of selection to secure the desired flock averages, close breeding must be employed with selection. Selection alone, even for strongly inherited characters, can only remove variation at such a slow rate that attention is more profitably devoted to other things. In Fleece Weight, for example, variation per se is unimportant. The suggestion that a good average grading in type of sheep and wool can be attained fairly quickly by breeding, but that elimination of variability is the work of a lifetime is, of course, in accord with practical experience.

The fact which stands out most from the results is the surprisingly low intensity of inheritance found for factors directly affecting returns from sheep and wool. Although these figures are low, they are of the same order as those found elsewhere for similar features in farm livestock. The genetic to total variance ratio for butterfat production in dairy cattle within herds, for example, ranges from .2 to .3, according to the number of lactations, studied in dam and daughter (Ward and Campbell 1940, Lush 1943), but only half of this can be utilised in practice because production cannot be measured in males. No comparable figures exist for the Romney sheep, but in Romney cross Rambouillet, Rasmussen (1942), estimates the heritability of Fleece Weight at about .14. Rasmussen's figures for straight Rambouillet and Canadian Corriedales are .40 and .26 respectively. Phillips et alia (1940) found high values for Fleece Weight inheritance in fine wool breeds, and it certainly does appear likely that the amount of wool produced by Romneys is less easy to improve by mass selection.

For characters inherited weakly, selection of superior stock for breeding, within a population limited to our better studs, can produce only slow results. It has been calculated, for example, that even all-out selection for Fleece Weight would take twenty to twenty-five years to produce an increase of one pound (McMahon 1940). In the case of selection on the female side, where not many young animals can be discarded if flock numbers are to be maintained, the effect is slow enough to be completely neglected. Ewe hoggets, then, especially in grade flocks, should be culled on features likely to influence returns during their own lifetime, rather than in terms of permanent flock improvement (Canterbury Chamber of Commerce 1942).

3. Progeny Tests of Rams:

Where the ratio of genetic variance to total variance is low the real breeding worth of an animal cannot be recognised, and breeders are often deceived in selecting for excellence. One way of minimising this source of error is to judge an animal not on its own appearance, but on the appearance or production of a number of its progeny. In this way, errors due to the deceiving effects of environment are spread over a number of individuals and tend to cancel. Moreover, when the number of offspring exceeds four or five the sampling process bound up with the formation of germ cells ensures that the progeny group contains a practically complete set of all the parent's genes. It gives, therefore, a direct appraisal, which becomes more and more accurate as the number of progeny increases, of the breeding worth of the animal.

In sheep, progeny testing is only possible on the male side, for progeny tests of females cannot normally be based on enough offspring for the sampling errors of reduction division to cancel out. By the time the number of offspring has become usefully large, the ewe is too old to be retained in the flock. So-called progeny tests of females are nearly all meaningless: firstly, because errors of appraisal are only little reduced when averaged over two or three sheep, and secondly, because a few offspring can contain only an inadequate sample of the parents' genes. To talk of "nicking" on the evidence of two or three progeny of a particular mating is even more ridiculous, for here sampling in both parents comes into the picture.

Although measurement of excellence is difficult with sheep, there are certain features of normal flock management which make the progeny testing of stud rams a very practical and accurate procedure, especially in large flocks. Most studs of reasonable size normally utilise from ten to twenty sires in one year, and the progenies are all raised together under the one set of conditions. There is no correlation between progeny group and special environment, such as is found when daughters of different dairy bulls are raised in separate herds, to hinder the accurate comparison of many sires at a time. The greater the number of sires which can be tested together, the greater the scope for selection, for efficiency is lost through evaluation of differences in environmental conditions never being very accurate. Where all the sires are tested together, too, simplicity is gained by neglecting the appearance of the dam because in characteristics where the progeny test is necessary, appearance is such a poor guide to breeding that the dams' effects on the progeny test are of no importance. Naturally, the dams for each sire must be a reasonable sample of the population, but once this has been established the progeny group becomes the unit in which we must deal, and its average value for each feature gives a simple basis for the comparison of rams.

Concentrating, then, on the sires' progeny groups, the analyses of variance used in calculating the intra-sire correlations for Table 2. readily establish the highly significant nature of differences among sire means. From the same analyses a measure of the rate of improvement possible using the progeny test can be obtained from the component of variance associated with differences between sires, while from the "within sires" term we can calculate the number of progeny necessary to give progeny tests with any required degree of accuracy. Table 3. shows how all this works for one group of progeny in the case of Fleece Weight.

TABLE 3.

ANALYSIS OF VARIANCE FOR FLEECE WEIGHT
Voss Ewe Hoggets of 1939.

Source	Degrees of Freedom	Sums of Squares	Mean Squares	Estimates of
Total	724	2163.1	2.988	
Between sire Groups	24	191.6	7.983	$\sigma_e^2 + \frac{725}{25}\sigma_s^2$
Within sire Groups	700	1971.3	2.816	σ_e^2

$F = \frac{7.983}{2.816} = 2.838$ Highly significant

In Table 3., σ_e^2 is the variance of a population of offspring all by one sire, and σ_s^2 is the variance of a population of accurate progeny tests of sires. We have:

$$\frac{725}{25}\sigma_s^2 + \sigma_e^2 = 7.983$$

$$\sigma_e^2 = 2.816 \text{ and } \sigma_e = \pm 1.677 \text{ lbs.}$$

$$\text{whence } 29.0\ \sigma_s^2 = 5.167$$

$$\text{so that } \sigma_s^2 = .178 \text{ and } \sigma_s = \pm .422 \text{ lb.}$$

The figure for variance associated with differences between the progeny tests of many sires (σ_s^2) is an estimate of the true effects of sires, separated from random errors due to each sire's mean value in the present data being based on a relatively small sample. Table 4. records the mean results for the two estimates of σ_s^2 and σ_e^2, and the corresponding standard deviations, over all the animals included in the present project. The "between sires" components (σ_s^2) have not been corrected for unequal numbers in the progeny groups. For this reason and because some groups will have had different environmental conditions despite indications to the contrary, the values obtained are probably somewhat high. Discounting for these facts by 10 per cent. still leaves plenty of scope for improvement by selection among sires, on the basis of their progeny tests.

TABLE 4.

Feature Studied	Between Sires				Within Sires		
	df.	σ_s^2	$.9\ \sigma_s^2$	$.95\ \sigma_s^2$	df.	σ_e^2	σ_e
Based on data from Voss Flock only:							
Head Grading	65	.008	.007	±.085 grade	1683	.618	±.786 grade
Breed Type	62	.029	.026	±.161 "	1586	.592	±.770 "
Fleshing	61	.027	.024	±.156 "	1563	.675	±.822 "
Wool Character	64	.033	.030	±.172 "	1705	.694	±.833 "
Count	64	.018	.016	±.130 count intervals	1707	.384	±.620 count intervals
Fleece Weight	65	.183	.165	±.406 lbs.	1665	2.590	±1.609 lbs.
Based on data from Matthews Flock and Voss Flock:							
Wool Character	93	.027	.024	±.156 grade	2246	.637	±.798 grade
Count	93	.014	.013	±.112 count intervals	2250	.360	±.569 count intervals
Fleece Weight	93	.220	.198	±.445 lbs.	2182	2.636	±1.624 lbs.

Figure 1 shows the expected superiority of the best sire for any given number tested, based on the "discounted" standard deviations for between sires ($.95\ \sigma_s$) of Table 4. (The "discounted" variance was not used in the calculations for Table 2.) Although the rate of improvement continues to increase as more and more sires are tested, it is clear that relatively less return is obtained from testing more than about 20 sires. This diagram gives a rough comparison of the amount of gain still to be had from progeny testing after normal selection of sires has taken place.

Turning now to the number of offspring necessary to prove each sire, Figure 2 shows how the reliability of the mean value for the sire group increases as the number of progeny considered grows larger. Statistically these are standard errors, and to establish significant superiority at 5 per cent. (odds 19 to 1) the mean of a sire's offspring must exceed the flock average by about twice the value shown.

Here again the amount of information gained decreases very rapidly after the first few offspring have been observed. In the case of Fleece Weight for sheep raised under stud conditions, fifteen progeny are sufficient to establish the superiority of a ram leaving fleeces .8 pounds above average, with odds of nineteen to one. One such ram should be found in about every 20 tested.

Fig. 1.

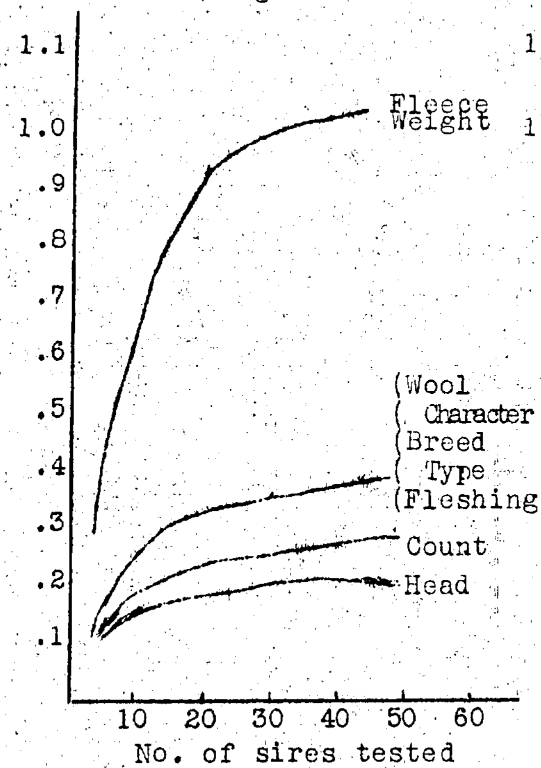
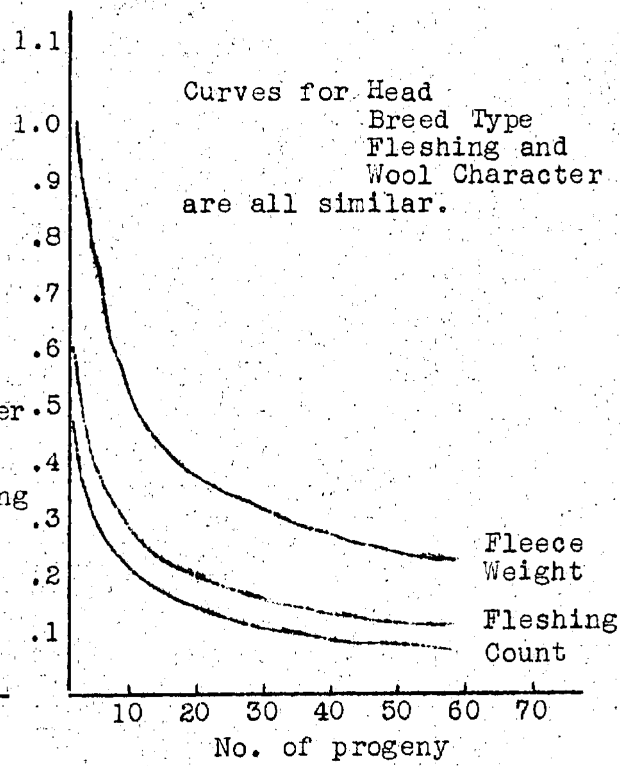


Fig. 2.



The ordinates are fractions of Count intervals, Grades or Pounds.

4. Repeatability of Progeny Tests:

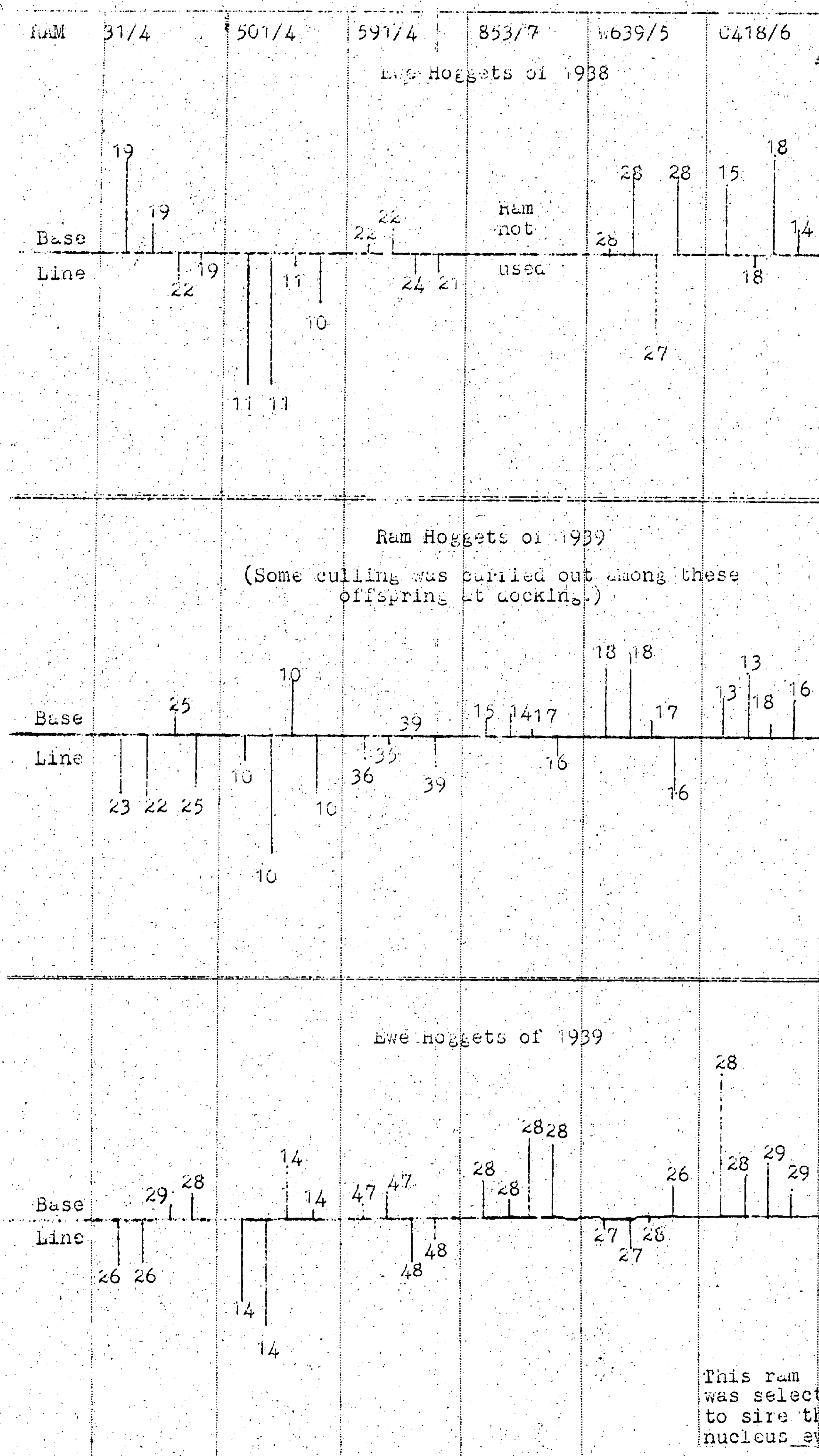
Our present data, being derived from three different sets of offspring, namely Ewe Hoggets of 1938, Ewe Hoggets of 1939, and Ram Hoggets of 1939, enable a check to be obtained on the repeatability of independent progeny tests. Table 5. records some of the possible correlations between repeat tests on the same sires for the various features studied.

TABLE 5.

Feature Studied	Correlation Between Tests Based on:			
	Ewe Hogs 1938	Ewe Hogs. 1939	Ewe Hogs. 1939	Ram Hogs. 1939
	Number of Pairs	Correlation	Number of Pairs	Correlation
Head Grading	11	.521	24	.482
Breed Type	12	.241	26	.643
Fleshing	12	-.066	26	.496
Wool Character	12	.038	26	.165
Count	12	.134	26	.496
Fleece Weight	13	.515	26	.428

These correlations are not high because the actual progeny tests utilised can in no case be completely accurate. The average offspring indeces contain sampling errors, the size of which will depend on the number of offspring actually observed. These errors do not interfere with the average returns from progeny testing calculated from the "between sires" standard deviations of Table 4., but they do make individual progeny tests less reliable.

It is not possible to reproduce here the whole of Figure 3 as originally presented. Data are given for only a few of the rams tested.



EXPLANATIO

The base line for each hog group is the mean all anim examined that grou The lines for each sire indi cate how much his average progeny w better or worse tha the mean of the group. The four lines giv results for Breed Type, Fle ing, Wool Character and Fleec Weight in that orde The verti cal scale ~~is about~~ 5cm. for grade an 2.5cm. fo 1lb. of fleece. The figu at the h of each show the numbers offsprin on which the test is based

Figure 3. shows a simple way of presenting results of progeny tests in terms of distance above or below the average of the whole flock reached by the progeny of any particular sire. Figure 3. also emphasises what is quite the biggest difficulty facing the would-be sheep improver. Even among so many rams tested, only one shows consistent superiority in all characters and in each batch of progeny examined, although two others appear sufficiently promising to be retained for further trial.

The rate of progress with any method of selection is inversely proportional to the square root of the number of characters which must be considered and it is clear thatnon-essential breed points must be entirely neglected. For factors of real productive value, Hazel and Lush (1942) have recently calculated the relative efficiency of selecting for several characters, one at a time; by the method of independent culling levels; and on the basis of a total score for excellence considering all factors together. They emphasise the increased efficiency of the total score method where culling cannot be intense, while pointing out that if only a few animals need be retained, it has small advantage over the method of independent culling levels. For calculating the most efficient combination of features for either of these methods, it is necessary to have information on heritability, on correlations existing between features, and on the relative economic values of the characters concerned. In the present study the first of these objects has been achieved and some of the possible correlations have been explored between different features on the one animal. In practice, a reasonable approximation to the total score method can be obtained from simple inspection of information presented in Figure 3., but until more correlations of different features on the same animal are worked out, it is not possible to formulate exact selection indeces for sheep.

Although for academic completeness, more correlations between features are required, the analyses presented in this paper suggest that the most efficient breeding programme for flocks such as those examined, would consist essentially of a Hagedoorn nucleus with the major part of the flock serving mainly as a trying-out ground for those sires which were candidates for nucleus honours. Not all sires bred in the nucleus could be progeny tested and in selecting the best rams for trial, more attention would be paid to features strongly inherited, such as Head Grading, Skeleton Formation and Wool Count. For features not strongly inherited, such as Fleece Weight, Fleshing and Wool Character, less attention would be given at the preliminary selection and more attention paid to the results of breeding tests. Probably, in the first instance, a single sire nucleus could not safely be established and three or four candidates would have to be considered. For these, the following sorts of mating should be tried:-

(1) To their own best daughters and best close relatives as a test of the inbreeding capabilities of the strain; to fix desirable genes; and to reduce variability.

(2) Remaining daughters and close relatives of one nucleus ram to other nucleus rams, i.e. no inbreeding, to concentrate desirable genes.

(3) The remaining mates for nucleus rams selected as best on appearance and performance from the rest of the flock.

In this way, only those sires graded high on progeny tests would be inbred and the final nucleus sire would not be chosen until it was established, by mating to his own daughters, that his hereditary make-up did not contain deleterious, recessive genes.

SUMMARY:

(1) Statistical analyses suggest that experienced sheep and wool men, when culling, utilise less than half the scope for selection which actually exists in the flock.

(2) With the exception of Count (Fibre Fineness) and desirability of Head Shape, the heritability fraction for the major factors influencing economic returns from sheep is less than .2.

(3) Selection for characters weakly inherited and for uniformity in features like type of Head and type of Wool, can give only a very slow return in terms of flock improvement; the effect on subsequent generations of the amount of selection normally possible among females is negligible.

(4) For characters inherited strongly, selection of sires gives opportunity for achieving high average gradings rapidly, but to secure uniformity, close breeding is essential along with selection.

(5) For characters inherited only weakly the progeny test gives opportunities for relatively spectacular improvement.

(6) A system of mating is described for medium and large flocks which makes the most efficient use of information which could be made available to a systematic breeder.

ACKNOWLEDGMENTS:

No account of the present project can be complete without acknowledgment of the assistance received from numerous workers who helped in the collection of data. Special mention must be made of Miss E. Arthur of Massey Agricultural College who so carefully checked the original gradings and pedigrees and of Misses Williamson, Shankland, and Collins, on whom has fallen the tedious routine of calculation. Finally, our best thanks are due to Messrs H. and M. Voss and Mr R.W. Matthews for their generous assistance and hospitality throughout the work.

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DISCUSSION.

Dr J.F. Filmer: Suggested that breeding beef cattle for characters very similar to those studied in the paper, had resulted in some of the modern strains being unable to produce sufficient milk to rear