RELATIONSHIPS AMONG PRODUCTIVE CHARACTERS OF MERINO SHEEP IN NORTH-WESTERN QUEENSLAND

2. ESTIMATES OF GENETIC PARAMETERS, WITH PARTICULAR REFERENCE TO SELECTION FOR WOOL WEIGHT AND CRIMP FREQUENCY

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SUMMARY

Estimates of heritability and genetic correlations among 10 fleece characters were obtained from a flock of Merino sheep at Toorak Field Station, Julia Creek.

Crimp frequency and fibre diameter had the highest heritability (0·57 in each case). The heritability of clean wool weight was estimated at 0·34. This character was highly correlated (negatively) with crimp frequency.

Assuming that the price of wool increases by approximately 3 per cent. for an increase of one crimp per inch, selection based solely on clean wool weight is recommended.

I. INTRODUCTION

A general review of the literature on heritability and genetic correlations among wool production characters was made by Turner (1956). Since then, Young, Turner, and Dolling (1960) have presented estimates of the heritability of 10 traits measured in a flock in southern Queensland. Genetic correlations estimated from the same data were discussed by Turner (1960) in relation to other estimates for the Australian Merino by Morley (1955) and Schinckel (1958).

Among other findings, these authors have all reported a consistent positive genetic association between clean wool weight and staple length but a moderate to strong negative correlation of both characters with crimp frequency. Estimates of heritability have been consistently high (most have been in the range 0·3 to 0·5), and any single character can be expected to respond to mass selection. In the flocks studied by Morley (1955) and Young, Turner, and Dolling (1960), responses of the order predicted have in fact been achieved in paired single character selection groups.

However, even when moderately large numbers of animals are studied the standard errors of the various genetic statistics are sufficiently large to make quite wide the fiducial interval of the difference between estimates of the same

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parameter in different flocks. This becomes a major problem when selection for more than one character is contemplated. For this reason, further estimates are desirable to confirm the general applicability of recommendations arising from the findings already published. This paper presents a set of estimates obtained from a flock in north-western Queensland.

Since crimp frequency is the measured character most closely related to price per pound, an attempt is also made to derive from these genetic statistics an optimum selection procedure based on clean wool weight and crimp. This point was discussed by Morley (1955) and Dunlop and Young (1960), using selection index theory, but in this study independent culling levels are considered since this is the procedure currently being advocated in most extension literature on fleece measurement.

II. MATERIAL AND METHODS

(a) Data and Methods of Analysis

The environment, the sheep and the characters measured were described in the first paper of this series (Beattie 1961). Numerous sets of dam-offspring pairs were formed so that in each set the dams were homogeneous with respect to age, year of record and as far as possible fecundity status. The offspring were similarly homogeneous with respect to age, year of record, sex (only a small proportion of male offspring were included) and sire (in those cases where mating was other than random).

Following the argument of Young, Turner, and Dolling (1960), heritability was estimated by doubling the dam-offspring correlation coefficient. Since no ewe culling is practised in this flock, this procedure was expected to remove any bias due to multiplicative effects without introducing any bias due to dam selection. For the same reason, the genetic correlations were estimated by the method of Hazel (1943), using the geometric mean in preference to the arithmetic mean in the numerator.

Fiducial limits for the estimates of heritability were calculated from Fisher's (1946) table of the "z" transformation and standard errors of the genetic correlations by the method of Reeve (1955).

(b) Selection using Independent Culling Levels for Wool Weight and Crimp Frequency

The phenotypic correlation between clean wool weight and crimp frequency in this flock has been estimated as $p = -0 \cdot 45$ (Beattie 1961). If this figure is accepted as a starting point, the question of optimum selection procedure for these two characters can be examined. It is assumed that truncation selection is to be employed, that is, the sheep selected are to be above certain minimum levels in both characters. It is also assumed that the two variates measured on parent and offspring form a 4 – normal distribution.

Let x_1 = clean wool weight of parent
x_2 = crimps per inch of parent
y_1 = clean wool weight of offspring
y_2 = crimps per inch of offspring

where all variates are measured in units of standard deviation as deviations from their means with heritabilities respectively h_1^2 and h_2^2 and genetic correlation r. It is also convenient to define

$$k^2 = \frac{h_1^2}{h_2^2}$$

If the relative economic values of clean wool weight and crimp frequency are known, that is

$$e = \frac{\text{economic value of standard deviation of clean wool weight}}{\text{economic value of standard deviation of crimp}}$$

the net merit of the offspring = $H = e\,\hat{y}_1 + \hat{y}_2$, where $\hat{y}_1$ and $\hat{y}_2$ are the expected offspring means.

Defining : Z (t) = univariate normal ordinate at t
Q (t) = univariate normal frequency above t
P = frequency in region with lower bounds

$$x_1 = a, \quad x_2 = b, \quad p = -0{\cdot}45$$

$$A = \frac{b + 0{\cdot}45a}{\sqrt{1 - (-0{\cdot}45)^2}}$$

$$B = \frac{a + 0{\cdot}45b}{\sqrt{1 - (-0{\cdot}45)^2}}$$

it can be shown (Beattie 1962) that H has a stationary value when a and b are the solutions of

$$P = \text{constant}$$

$$\frac{Z(A)}{Q(A)} - A = T\left\{\frac{Z(B)}{Q(B)} - B\right\}$$

where

$$T = \frac{X + 0{\cdot}45Y}{Y + 0{\cdot}45X}$$

$$X = k\,(ek + r)$$

$$Y = 1 + erk$$

Since X and Y cannot both be negative, assume X is positive (a similar argument can be applied assuming Y is positive).

It is found that there are four cases :

(i) $\frac{X}{Y}$ positive or less than $-2{\cdot}2^{\cdot}$; the equations above give a maximum for H.

(ii) $O > \frac{X}{Y} > -0{\cdot}45$; the equations above give a minimum for H ; upper limit is at $b = -\infty$

(iii) $-0{\cdot}45 > \frac{X}{Y} > -1{\cdot}0$; H has no stationary value ; upper limit at $b = -\infty$ is numerically less than lower limit at $a = -\infty$

(iv) $-1{\cdot}0 > \frac{X}{Y} > 2{\cdot}2^{\cdot}$; H has no stationary value ; upper limit at $b = -\infty$ is numerically greater than lower limit at $a = -\infty$

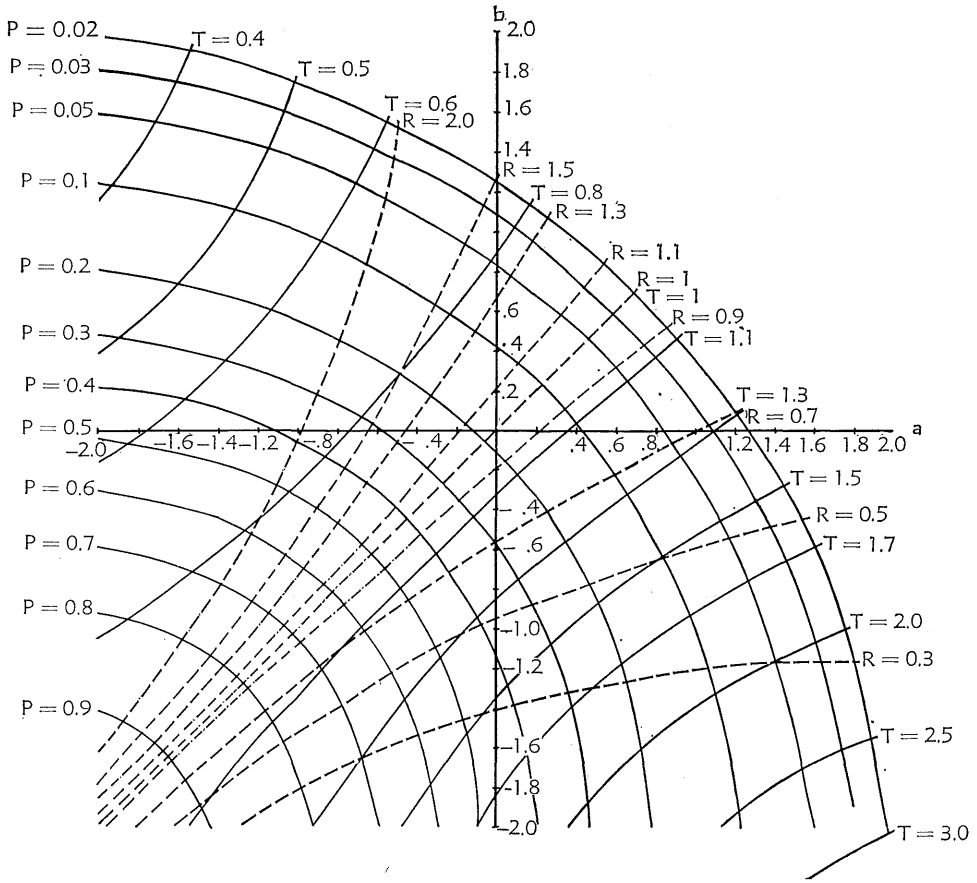

Fig. 1.—Values of P, R, T for normal distribution truncated at a and b assuming $p = -0{\cdot}45$. For meaning of symbols see text.

If the initial proposal is adhered to (all selection to be in the positive direction), cases (ii), (iii) and (iv) indicate that x_2 should be ignored and all selection applied to x_1. However, it is clear that more effective procedures are possible, particularly in cases (ii) and (iii).

Using the above results, Figure 1 was constructed with the aid of Pearson's (1930, 1931) tables. For a and b as arguments, this figure is a P, T, R grid, where P and T have been defined above. The R curves determine a and b such that the expectation of y_2 is zero. This condition implies $R = -rk = \dfrac{Z(b)\,Q(B)}{Z(a)\,Q(A)}$

If $\hat{u}_1$ = expectation of y_1 subject to $\hat{y}_2 = O$

$\hat{v}_1$ = expectation of y_1 under unrestricted selection for x_1

it is easily seen that

$$\frac{\hat{u}_1}{\hat{v}_1} = (1 - r^2)\,\frac{Z(a)\,Q(A),}{Z(c)} \quad \text{where } Q(c) = P$$

III. RESULTS AND DISCUSSION

(a) Heritability

Estimates of the heritability of the 10 characters are shown in Table 1. The range in heritability is from 0·26 for one of the fold scores to 0·57 for crimp frequency and fibre diameter. The general agreement with other published figures for the Merino is quite good. For wool weight (greasy and clean) the

TABLE 1

ESTIMATES OF HERITABILITY

Character	Heritability	95% Fiducial Interval
Greasy wool weight	0·35	0·17–0·53
Per cent. clean scoured yield . .	0·40	0·22–0·57
Clean wool weight	0·34	0·15–0·51
Fibre diameter	0·57	0·39–0·73
Coefficient of variation of fibre diameter	0·43	0·26–0·61
Staple length	0·50	0·33–0·67
Crimps per inch	0·57	0·40–0·74
Body weight	0·54	0·34–0·74
Neck score	0·26	0·05–0·47
Side score	0·30	0·09–0·51

—	First 7 Characters	Last 3 Characters
Degrees of freedom	469	332

estimates are somewhat lower than those of Morley (1955) but intermediate between those for yearling rams and 15–16 month ewe and ram offspring given by Young *et al.* (1960). The estimate for crimp frequency is somewhat higher than the figures given by these authors. On the other hand, the estimates for the two fold scores are lower but comparable with Schinckel's (1958) estimate of 0·27.

(b) Genetic Correlations

The genetic correlation coefficients are listed in Table 2. The estimates are above the diagonal and standard errors below the diagonal. As shown by these standard errors the estimates are of rather low precision. The calculated correlation between the two fold scores exceeds unity (this can be interpreted as support for the view that the neck and side scores are effectively estimates of the same attribute), and some of the other high correlations are probably similarly inflated by sampling variation or unrecognized sources of bias. Nevertheless, there is reasonable agreement with the findings in the three flocks discussed by Turner (1960). In particular, there is full agreement on the signs of the following genetic associations:—

Clean wool weight with yield, staple length and fibre diameter (positive).

Clean wool weight with crimp frequency (negative).

Crimp frequency with body weight and fold score (positive).

Crimp frequency with fibre diameter, staple length and yield (negative).

Body weight with fold score (negative).

Fold score with fibre diameter (positive).

Fold score with staple length (negative).

(c) Optimum Selection Based on Clean Wool Weight and Crimp Frequency

The notation of Section II b is used without further definition.

From Table 2, the coefficient of genetic correlation between clean wool weight and crimp frequency is highly negative, $r = -0 \cdot 96$. From Table 1 the ratio of the heritabilities of clean wool weight and crimp frequency is $\frac{0 \cdot 34}{0 \cdot 57} = 0 \cdot 60$, i.e. $k = 0 \cdot 77$.

An estimate is required for the relative economic value of one standard deviation of each character. In the first paper of this series (Beattie 1961) the mean clean wool weight in this flock was estimated as 4·50 lb with coefficient of variation 17·3 per cent. The corresponding estimates for crimps per inch were 12·2 and 18·5 per cent. Dunlop and Young (1960) estimated the regression coefficient of price per pound on crimp as 3·08 per cent. per crimp. Accepting their figure and combining it with the phenotypic statistics, the value

TABLE 2

GENETIC CORRELATIONS* AMONG CHARACTERS

Character	Greasy Wool Weight	Per cent. Clean Scoured Yield	Clean Wool Weight	Fibre Diameter	C. of V. of Fibre Diameter	Staple Length	Crimps per Inch	Body Weight	Neck Score	Side Score
Greasy wool weight	..	+0·06	+0·82	+0·19	+0·15	+0·70	−0·87	+0·20	−0·15	+0·09
Per cent. clean scoured yield ..	±0·26	..	+0·64	+0·03	+0·09	+0·54	−0·47	+0·11	−0·47	−0·49
Clean wool weight	±0·10	±0·17	..	+0·16	+0·15	+0·89	−0·96	+0·33	−0·49	−0·28
Fibre diameter	±0·20	±0·18	±0·21	..	+0·11	−0·11	−0·17	−0·00	+0·30	+0·09
Coefficient of variation of fibre diameter	±0·21	±0·19	±0·22	±0·15	..	+0·04	−0·42	+0·18	−0·07	−0·10
Staple Length	±0·17	±0·15	±0·16	±0·14	±0·15	..	−0·75	+0·01	−0·44	−0·47
Crimps per inch	±0·20	±0·15	±0·19	±0·13	±0·14	±0·12	..	+0·15	+0·54	+0·27
Body weight	±0·24	±0·21	±0·24	±0·16	±0·18	±0·17	±0·18	..	−0·25	−0·12
Neck score	±0·35	±0·28	±0·41	±0·20	±0·22	±0·19	±0·24	±0·22	..	+1·22
Side score	±0·32	±0·32	±0·39	±0·22	±0·23	±0·21	±0·23	±0·24	±0·19	..

—	First 7 characters	Last 3 Characters
Degrees of Freedom ..	469	332

* Genetic correlation coefficients: above diagonal.
Standard errors: below diagonal.

of one standard deviation of clean wool weight can be taken as 77·85 and the value of one standard deviation of crimp frequency as 31·28. These estimates make e approximately 2·5.

For these values of e, r and k, X = +0·74 and Y = —0·85. This comes under case (iii). If positive selection is to be practised it should be directed entirely to x_1 (clean wool weight). However, selection against x_2 would be more efficient and in fact approach the efficiency of using the appropriate selection index ($0{\cdot}71x_1 - x_2$). These comparisons are set out in Table 3.

TABLE 3

RELATIVE PROGRESS UNDER THREE SYSTEMS OF SELECTION*

—	Clean Wool Weight	Crimps per Inch	Net Merit
Selection for clean wool weight	+0·34	—0·42	+0·43
Selection against crimps per inch	+0·42	—0·57	+0·49
Index selection	+0·45	—0·59	+0·54

* Assuming p = —0·45, r = —0·96, k = 0·77, e = 2·5

It is now necessary to consider the effect of errors in the estimates of p, e, r and k. Using methods adapted from Yates (1939), the approximate 95 per cent. fiducial interval for k is found to be from 0·53 to 0·99. The genetic correlation coefficient r, despite its standard error, is almost certainly highly negative and consideration of r in the range —1·0 to —0·4 is probably conservative. Figure 2 was constructed to show the variation in T with r and k over this domain (but still holding p at —0·45 and e = 2·5). The region to the left of T = —1·0 corresponds with case (iii) (selection against crimp frequency). The region between T = —1·0 and T = $\pm\infty$ corresponds with case iv (positive selection for clean wool weight). The region to the right of T = $\pm\infty$ corresponds with case (i) and the T curves of Figure 1 are appropriate.

If e is varied, an increase on the assumed value of 2·5 will move the curves to the right, a decrease to the left. Since p is presumably the best determined of the four variates, the result of variation in this parameter will not be considered.

At the end of Section II b an expression was derived for the efficiency of selection for clean wool weight, holding crimp constant compared with unrestricted selection for clean wool weight. For r = —0·96 and k = 0·77, R = 0·74. Efficiency increases with selection intensity but is always very low. Even when the retained part of the flock is as small as 2 per cent., efficiency is only 7 per cent. Assuming e = 2·5, the progress in net merit for this value of P is 15 per cent. of that which could be obtained by selection for clean wool weight alone. Using the selection index $x_1+0{\cdot}74x_2$, the corresponding figure, independent of P, is 17 per cent. The effect of errors in e, r, k have

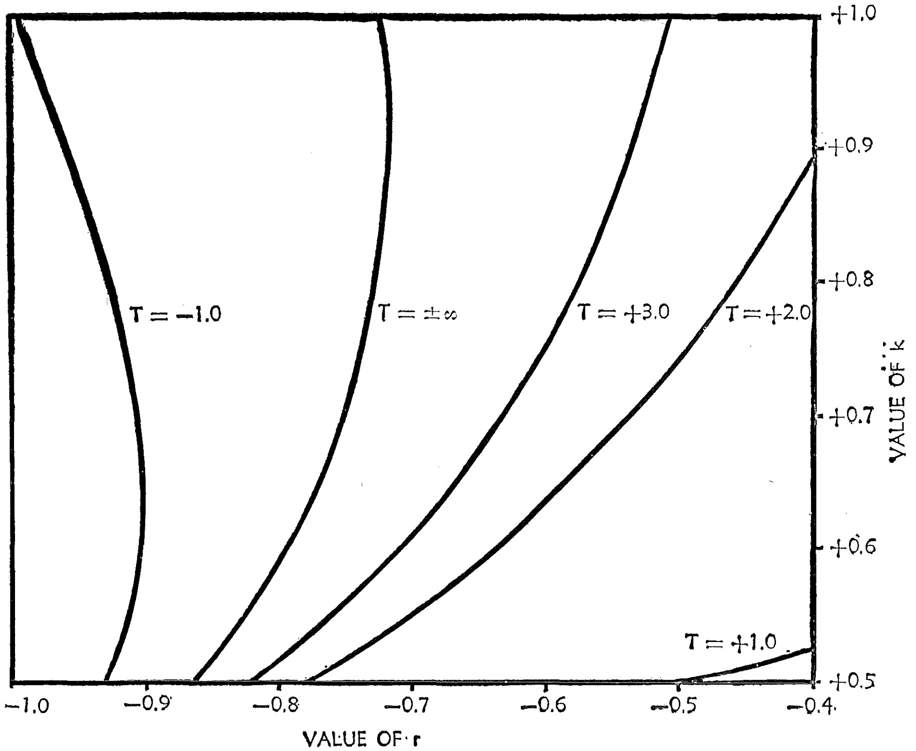

Fig. 2.—Values of T as function of k and r assuming p = −0·45 and e = 2·5. For meaning of symbols see text.

not been investigated in detail but it is obvious that a decision to hold crimp constant will markedly reduce progress in wool weight and net merit for a wide range of these parameters.

For this flock, it is concluded that any practical breeding programme aimed at improving cut per head and economic return will involve some strengthening of the wool as assessed by crimp. The greatest economic return is likely to come from selection for wool weight alone or even selection against crimp frequency. Under these circumstances there is likely to be a small increase in fibre diameter, but countering this, an increase in staple length and a probable decrease in fold development. Since the wool produced in north-western Queensland includes a large proportion of counts 64's and finer, this type of selection is practicable. However, the comments of Dunlop and Young (1960) are valid. Too large a swing towards a stronger clip could on the national scale lower the general price structure of the industry. Alternatively, or as well, it could increase the price advantage of finer wools.

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