

ASYMMETRY OF RESPONSE TO SELECTION FOR SKIN FOLD SCORE IN AUSTRALIAN MERINO SHEEP

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SUMMARY

The direct response achieved after 20 years of divergent selection for skin fold score was examined in relation to a randomly-selected control flock. An estimate of 0.56 was obtained for the heritability of fold score in the control flock. Selection response was asymmetric, giving a realised heritability of 0.36 in the upward direction and 0.53 in the downward direction. However, the latter flock was characterised by a reduction in the realised heritability estimate over time. This was concluded to be the result of large changes in gene frequency. On the other hand, the lower estimate obtained with upward selection was attributed to a failure to account for linkage disequilibrium in the regression of response on selection differential. The potential for misinterpretation of selection response when due consideration is not given to causal factors of asymmetric response is illustrated.

INTRODUCTION

Predictions of response to divergent selection assume an equal rate of response in both upward and downward directions. However, realised responses can often be asymmetrical, arising from factors such as random drift, differences in selection differential, inbreeding depression and changes in gene frequency (Falconer 1981). The implication of asymmetric responses in relation to sheep and other livestock animals is that genetic improvements in economically-important traits may fall short of expectation. To date, a number of sheep selection experiments have been conducted in which divergent flocks have been maintained in conjunction with a control flock (Purser 1979; McGuirk et al. 1986; Davis and McGuirk 1987), enabling asymmetry of response to be examined. This paper reports asymmetry of response to selection for skin fold score in Australian Merino sheep, with particular reference to changes in gene frequency expected to accompany selection for low skin fold score (Morley 1953).

METHODS

The selection experiment was initiated in 1951 by the NSW Department of Agriculture at the Trangie Research Station and continued for 20 years. Three flocks were established from a common base population: Folds(+), selected for high fold score; Folds(-), selected for low fold score; and a randomly selected control flock. Each flock consisted of approximately 100 ewes, mated annually to 5 rams (10-25 rams in the control) of 1½ years age. Skin fold scores were given off-shears at 4 months age according to the photographic standards of Carter (1943). Scores ranged from 1 (absence of folds) to 9 and were assigned to neck (N), side (S) and breech (B) regions. Base parents were selected on the basis of breech fold score only. From 1951 onwards, selection was based on the total score (though breech score was not recorded after 1961) and was continued until 1971. As the genetic correlations between N+S, N+S+B and the component scores are close to unity (Crook 1992), it has been assumed for simplicity that the selection criterion since 1951 was N+S score. All N+S scores were transformed to the log₁₀ scale (hereby denoted NSLOG) prior to analysis for reasons outlined by Morley (1953).

The heritability of NSLOG was estimated within each flock using the program DFREML (Meyer 1991) to fit a univariate individual animal model with a full numerator relationship matrix, together with year and sex as fixed effects. The within-flock estimate was then used as a prior for BLUP analysis to estimate breeding values (EBV) for that flock. Additional BLUP analyses of the Folds(+) and Folds(-) flocks were also made using the Random flock estimate of heritability as a prior.

Expected and realised selection differentials were calculated for each flock (Falconer 1981) as were the group cumulative selection differentials (GCSD) (James 1986). Annual trends in GCSD were examined by

regressing GCSD on year. Annual genetic changes in the Folds(+) and Folds(-) flocks were obtained by regressing annual response on year, with response being estimated by two methods: (i) annual mean fold score expressed as a deviation from the corresponding Random flock mean, and (ii) annual mean EBV. Realised heritabilities were calculated in the Folds(+) and Folds(-) flocks by regressing annual response (as defined by methods i and ii) on the appropriate GCSDs. All regressions were forced through the origin. The standard errors of estimates derived under method (i) account for drift variance, according to the method of Hill (1972). Realised heritabilities for method (i) responses were also obtained at years 1, 6, 11 and 16 to examine changes in the estimate with time.

RESULTS

The average generation interval in the Folds(+), Folds(-) and Random flocks was 3.16, 3.24 and 3.20 respectively. On average, 82% of Folds(+) ewes were selected as replacements as opposed to 53% in the Folds(-) flock, while 27.5% and 15.3% of rams were selected. At completion, approximately 7.3 generations of selection had been practised. Realised selection differentials on the ewe side were predominantly positive in the Folds(+) flock and all were negative in the Folds(-) flock. The ratio of realised to expected selection differentials in the Folds(+) flock declined with time from 1.20 to 0.70 though the ratio remained in excess of 0.96 in the Folds(-) flock. After 20 years selection, a total cumulative selection pressure of 3.40 and -4.25 standard deviations was achieved in the Folds(+) and Folds(-) flocks respectively. The average annual change in GCSD declined with time in both flocks, though more so in the Folds(+) flock. There was no directional change in the selection differentials in the Random flock.

When pooled over sexes, annual genetic response in skin fold score in the Folds(+) and Folds(-) flocks averaged 0.016 and -0.026 units (± 0.002) per year respectively (Figure 1). The annual rate of change in response declined with time in both flocks for regressions through the origin. However, the change in annual response per unit change in GCSD remained relatively constant over time in the Folds(+) flock, giving an estimate of 0.36 ± 0.06 for the realised heritability over the entire experiment (Table 1). On the other hand, the realised heritability in the Folds(-) flock declined throughout the experiment to give an estimate of 0.53 ± 0.06 at completion (Table 1).

REML estimates of heritability for skin fold score in the Random, Folds(+) and Folds(-) flocks were 0.56 ± 0.04 , 0.57 ± 0.08 , 0.37 ± 0.08 respectively. The associated additive genetic variances were 0.023, 0.020 and 0.010 units², and the phenotypic variances, 0.042, 0.035 and 0.026 units². Using the mean EBVs derived from these within-flock heritabilities, estimates of 0.013 and -0.011 were obtained for the annual genetic change in the Folds(+) and Folds(-) flocks respectively (Figure 2). Using the Random flock estimate of 0.56 did not significantly alter the genetic trend in either flock. The regression of mean EBV on GCSD gave a realised heritability of 0.30 in the Folds(+) flock and estimates of 0.23 and 0.33 in the Folds(-) flock (the latter derived using the Random flock estimate of heritability).

DISCUSSION

The asymmetry of response to selection for skin fold score supports the observations made by early breeders that it was easier to reduce the level of folds than to increase it (Austin 1950). This can be partially explained in the Trangie experiment by the relatively low selection intensity and thus lower GCSD's in the Folds(+) flock. The decline in the ratio of realised to expected selection differentials in this flock also implies that natural selection may have been antagonistic to selection for high skin fold score and was likely to have been operating by way of lower reproductive rate (Crook 1992). This would explain the decreasing change in GCSD over time. In the Folds(-) flock, the decline in rate of change in GCSD was due mainly to the non-random selection of base parents.

However, asymmetrical patterns in the realised heritabilities cannot be attributed to differences in selection differentials. The estimate of 0.36 in the Folds(+) flock and 0.53 in the Folds(-) flock suggests that the response to selection in the low line was in agreement with the Random flock estimate of heritability, while

Figure 1. Response to selection in NSLOG in the Folds(+) and Folds(-) flocks (averaged over sex), expressed as a deviation from the Random flock.

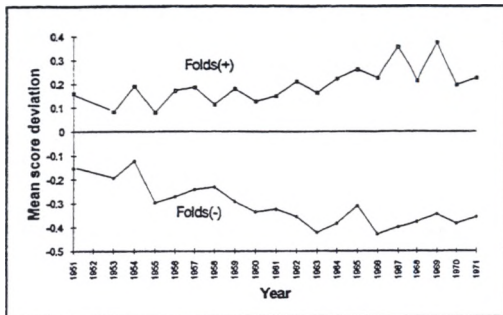


Figure 2. Mean estimated breeding values for NSLOG in the Folds(+), Random and Folds(-) flocks (averaged over sex).

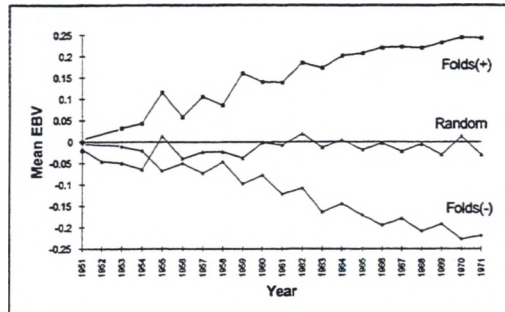


Table 1. Realised heritabilities for NSLOG at years 1, 6, 11, 16 and 21 in the Folds(+) and Folds(-) flocks. Realised heritabilities for divergence are also given. Standard errors are approximate, accounting for genetic drift.

	year				
	1	6	11	16	21
Folds(+)	0.62	0.41±0.07	0.34±0.06	0.34±0.05	0.36±0.06
Folds(-)	0.80	0.84±0.10	0.72±0.09	0.62±0.07	0.53±0.06
Divergence	0.70	0.60±0.04	0.51±0.03	0.48±0.02	0.45±0.02

response in the high line was lower than expected. As the regression of response on GCSD does not account for reductions in variance due to selection, realised heritabilities are expected to underestimate the base population value when the effects of linkage disequilibrium are appreciable. On the other hand, mixed model analyses of flocks undergoing selection can provide unbiased estimates of base population parameters if the full numerator relationship matrix is used and all information determining the selection decision is incorporated. This is because the model will account for changes in the genetic variance arising from genetic drift, inbreeding and linkage disequilibrium (Sorensen and Kennedy 1984). The REML estimate of heritability within the Folds(+) flock showed remarkable similarity to that in the Random flock whereas the estimate of 0.37 in the Folds(-) line was markedly smaller. It can therefore be concluded that the poor agreement between realised heritability in the Folds(+) flock and the Random flock estimate of 0.56 probably arose from a failure to account for linkage disequilibrium in the regression of response on GCSD. Thus the observed response in the Folds(+) flock was in accordance with predictions that allow for linkage disequilibrium.

The lower heritability and variance estimates in the Folds(-) flock and the associated decline in the realised heritability suggest that effects other than linkage disequilibrium, genetic drift and inbreeding were operating in this flock. Analyses by REML assume that the trait under selection is determined by an infinite number of unlinked additive genes, each of small effect, and that the frequencies of these genes do not alter under selection. This is the so-called "infinitesimal model" (Bulmer 1980). If this model does not hold, then estimates of heritability and genetic variance will become progressively smaller when derived from data sets with increasing numbers of generations, as was shown by Meyer and Hill (1991). Such a trend was reported by

Crook (1992) for the Folds(-) flock. It was thus concluded that the infinitesimal model was inappropriate for analysis of this flock due to suspected large changes in gene frequency. This also explains the smaller estimate of genetic change in this flock relative to the Folds(+) flock when derived from mean EBVs, regardless of the heritability estimate used, as estimation of these values assumes an infinitesimal model. A change in gene frequency after a few generations of selection suggests that skin folds is influenced by a small number of genes of large effect. In fact, the total response produced by divergent selection equated to no more than four times the original genetic standard deviation, indicating that the extreme genotypes were present in the base population at frequencies greater than those expected when a large number of loci are involved.

These results agree with the conclusions of Morley (1953) that selection for freedom from folds in the Merino would result in large changes in gene frequency, genetic variance and population mean.

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