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## Genetic parameters for improvement of dual-purpose flock productivity with constraints on mature ewe body weight

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### ABSTRACT

SIL provides opportunity for inclusion of information on mature ewe body weight in animal evaluations. This paper reports estimates of the parameters needed for these evaluations. Traits analysed were: weaning weight (WWT) and hogget liveweight in May (ALW); hogget yearling liveweight (HLW) and greasy fleece weight (HFW); and pre-mating body weights (ELW), number of lambs born (NLB) and greasy fleece weights of ewes at 2 to 5 years of age. EFW and especially ELW, were highly repeatable ( $>0.9$ ), the pattern of genetic correlations suggesting that breeding ewes had reached maturity in these traits by 40 months of age. Direct and maternal genetic effects on WWT showed similar heritabilities ( $0.14 \pm 0.02$  &  $0.18 \pm 0.02$ ) and were positively correlated ( $0.20 \pm 0.08$ ). Maternal influences on traits measured at old ages were much reduced, direct heritabilities being similar to published estimates. WWT showed a high direct genetic correlation with LW8 and HLW ( $0.82 \pm 0.02$ ), but lower with ELW ( $0.70 \pm 0.06$  for 3-year old ewes). LW8 and HLW showed even higher direct genetic correlations with ELW (of the order of  $0.90 \pm 0.02$ ). EFW was highly correlated genetically with HFW ( $0.80 \pm 0.03$ ), HLW ( $0.25 \pm 0.04$ ), ELW ( $0.23 \pm 0.05$ ) and LW8 ( $0.21 \pm 0.04$ ). Dual-purpose genetic response predictions were derived using SIL's recently revised relative economic values for a dual-purpose index. Its correlation with aggregate breeding value was 0.67. It predicted positive selection responses (per generation and standard deviation of selection pressure) in all traits: LW8 (2.1 kg), EFW (0.14 kg), NLB (0.038 lambs/ewe) and ELW (2.4 kg or 87% of the predicted single trait response despite the negative economic weight for this trait). Restraining the response in ELW to zero required a ten-fold increase in the negative relative economic value for this trait, and reduced the correlation of the index with aggregate breeding merit to 58% of its previous value. Such restriction greatly increased the relative contribution of fleece weight to economic response, made little difference to the contribution of NLB (although the absolute rate of progress was nearly halved), and reduced the contribution of growth; maternal effects on weaning weight became relatively more important.

**Keywords:** genetic parameters; hogget growth; wool and lamb production; ewe weight.

### INTRODUCTION

A new national sheep recording scheme developed by Sheep Improvement Limited (SIL), provides opportunity for inclusion of information on mature ewe body weight in animal evaluations for selection decisions by breeders (Geenty, 2000; Newman *et al.*, 2000). This paper reports estimates of genetic parameters needed for these evaluations with emphasis on the genetic relationships of mature ewe body weight with lamb and hogget growth and fleece production, ewe fleece weights and lamb production. Preliminary results on dual-purpose genetic response predictions to selection on an index of aggregate economic value are also presented, including indices aimed at restraining the response in ewe liveweight to zero.

### MATERIAL AND METHODS

Data came from four randomly selected control lines and a line selected on hogget body weight established in 1973 following two years of random mating among pedigree-recorded ewes and rams procured from more than 50 sources throughout the country and run at the Tokanui Research Station in the Waikato. Each line was represented each year by five two-tooth rams (single-sire pedigree matings) and 150 mixed-age ewes (two- to five-year-olds at their first lambing). Whenever possible each sire family generated one ram and a similar number of two-year old line replacements each year. Experimental management and data collection were as described by Clarke and Johnson (1993), Johnson *et al.* (1995), Clarke *et al.* 1995 and Morris *et al.* (1996). Animals from all lines were weighed at

weaning (WWT), shorn as lambs in December and as yearlings (HFW) the following September/October. Ram and ewe hoggets (HBW) and their fleeces were weighed (HFW) following shearing as hoggets at 14 months of age. Breeding ewes were weighed and mated for their first time at 19 months of age and annually for the following three years (EBW). They were shorn each year in December (EFW) and mated at random to one of the five two-tooth sires used to generate line replacements, but avoiding half-sib matings in the case of two-year-olds. Dry ewes were recorded (zero NLB); lambs from lambing ewes were identified with their mothers and tagged within 24 hours of birth.

Genetic parameters were estimated by fitting a restricted maximum likelihood, mixed animal model, using ASREML (Gilmour, 1997). In addition to random animal (average genetic) effects, some models also included random dam (maternal genetic) effects, repeated dam effects (without using the relationship matrix), and litter effects (within-year environmental effects of the dam on her progeny). Fixed non-genetic effects included in the model were: birth-rearing rank, age of dam and within-line birth day deviations for lamb and hogget traits; and year x sex effects and selection line effects for all traits. Both univariate and multivariate analyses were undertaken, the latter providing estimates of genetic and phenotypic correlations as well as of heritabilities, and allowing for the effects of selection on HBW in one of the lines.

**TABLE 1:** Base data, single-trait heritability estimates and associated variance ratios

Trait	$h^2_d$	$h^2_{dm}$	$h^2_m$	$pe^2$	$c^2$	sd	mean	n
Single-trait model								
WWT	0.14±.02	0.01±.01	0.12±.02	0.07±.01	0.20±.01	3.48	20.7	16589
ALW	0.41±.03	-.01±.01	0.07±.01	-	-	4.79	34.0	15320
	0.45±.02	-	-	-	-			
HBW	0.42±.02	0.03±.01	0.03±.01	-	-	5.89	45.3	14529
	0.49±.02	-	-	-	-			
EBW <sub>3</sub>	0.41±.03	-	-	-	-	5.98	49.7	5390
HF <sub>W</sub>	0.36±.02	-	-	-	-	0.338	3.49	14493
EFW <sub>3</sub>	0.42±.03	-	-	-	-	0.329	4.03	4473
NLB <sub>3</sub>	0.06±.02	-	-	-	-	0.620	1.11	5286
Two-trait model (including direct genetic effects for HBW)								
WWT	0.14±.02	0.03±.01	0.18±.02	0.03±.01	0.15±.01	3.50		
ALW	0.42±.03	-	0.08±.01	-	-	4.81		
	0.47±.02	-	-	-	-	4.80		
EBW <sub>3</sub>	0.43±.02	-	-	-	-	6.40		
HF <sub>W</sub>	0.36±.02	-	-	-	-	0.586		
EFW <sub>3</sub>	0.42±.03	-	-	-	-	0.581		
NLB <sub>3</sub>	0.06±.02	-	-	-	-	0.619		

$h^2_d$  = direct heritability,  $h^2_m$  = maternal heritability,  $h^2_{dm}$  = direct/maternal covariance as a proportion of the phenotypic variance;  $pe^2$  = permanent non-genetic dam effects as a variance ratio after allowing for  $c^2$  (litter variance as a proportion of phenotypic variance); sd = phenotypic standard deviation; 3 = three year-old record

## RESULTS

### Single trait estimates

Unadjusted means and phenotypic variances and single trait estimates of heritabilities (direct, maternal and the covariance between them as a proportion of phenotypic variance) are presented in Table 1. For comparison, estimates coming from two-trait runs including HBW, are also presented.

Permanent non-genetic (across-year) effects of the dam and litter (within year) effects of the dam were important only for WWT. Inclusion of significant maternal components of variation for lamb traits reduced the estimates of direct heritability. Estimates of maternal components of variation were only slightly affected by inclusion of HBW in the model – genetic estimates were increased and environmental estimates reduced. The heritabilities of direct and maternal genetic effects on WWT were similar.

### Multiple-variate estimates

#### Maternal genetic effects on growth

A comparison of multiple-trait estimates of heritabilities and correlations, with and without the inclusion of maternal genetic effects in the model, is presented in Table 2. Differences were most marked for WWT estimates.

Estimates of heritabilities from multiple trait analyses were similar to those from the corresponding single trait runs. Heritabilities of maternal genetic effects on liveweights declined from the small positive estimate (0.15) obtained at weaning. Covariances with corresponding direct genetic effects were small, but moderately positive between maternal effects at weaning and direct genetic effects at later ages. Estimates of direct genetic correlations among lamb and hogget liveweights tended to be lower when maternal genetic effects were included in the model and closer to corresponding phenotypic values.

**TABLE 2:** Comparison of multiple trait estimates of heritability (on diagonal in bold type), phenotypic (above diagonal) and genetic correlations (below diagonal) for lamb and hogget liveweights with (bottom row) and without (top row) inclusion of maternal genetic effects in the model\*

	WWT <sub>d</sub>	WWT <sub>m</sub>	ALW <sub>d</sub>	ALW <sub>m</sub>	HBW <sub>d</sub>	HBW <sub>m</sub>
WWT <sub>d</sub>	<b>0.33±.02</b>	-	0.67±.01	-	0.60±.01	-
	<b>0.15±.02</b>		0.72±.01		0.66±.01	
WWT <sub>m</sub>	-	-				
	0.20±.08	<b>0.15±.01</b>				
ALW <sub>d</sub>	0.83±.01	-	<b>0.47±.02</b>	-	0.83±.01	-
	0.77±.03	0.48±.05	<b>0.42±.03</b>		0.85±.01	
ALW <sub>m</sub>	-	-	-	-		
	-.01±.09	0.66±.06	-.06±.07	<b>0.05±.01</b>		
HBW <sub>d</sub>	0.81±.02	-	0.94±.01	-	<b>0.49±.02</b>	-
	0.74±.03	0.63±.04	0.89±.01	0.85±.05	<b>0.41±.02</b>	
HBW <sub>m</sub>	-	-	-	-	-	-
	0.07±.13	0.89±.06	0.19±.12	0.27±.13	0.31±.11	<b>0.03±.01</b>

\* subscript d indicates direct, and m maternal genetic effects;  $pe^2$  for WWT = 0.03,  $c^2$  = 0.15.

### Adult traits

Fitting a multivariate model (within lines) to the repeated annual expressions of pre-mating ewe liveweight (EBW) at two- to five-years of age gave high estimates of genetic correlations (0.90 to 0.99), especially among liveweights at three- to five- years of age (0.98 to 0.99). The genetic correlations of two-year records with later records were similar and averaged 0.93±.02. Results suggested that three-year-old records reflect genetic differences in mature ewe liveweight, although the estimates of heritability at this age tended to be a little higher than at later ages (0.41±.02, 0.37±.03 and 0.38±.03, for three- to five-year-olds respectively).

Fitting a multivariate model to adult fleece weights, by contrast, did not demonstrate such an age-related pattern to inter-age genetic correlations, the average genetic correlation among two- to five-year-old records being 0.96±.02 and the average heritability 0.43±.03.

Similar analyses suggested that a repeatability model

**TABLE 3:** Multiple trait estimates of heritability (on diagonal in bold type), phenotypic (above diagonal) and genetic (below diagonal) correlations\*

	WWT <sub>d</sub>	WWT <sub>m</sub>	ALW	HBW	HFW	ELW <sub>3</sub>	EFW <sub>3</sub>	NLB <sub>2,4</sub>
WWT <sub>d</sub>	<b>0.16±.02</b>	-	0.73±.01	0.66±.01	0.40±.01	0.49±.01	0.23±.02	0.07±.02
WWT <sub>m</sub>	0.30±.08	<b>0.12±.02</b>	-	-	-	-	-	-
ALW	0.77±.03	0.68±.04	<b>0.45±.02</b>	0.84±.01	0.59±.01	0.63±.01	0.27±.02	0.11±.02
HBW	0.75±.04	0.63±.04	0.92±.01	<b>0.47±.02</b>	0.62±.01	0.72±.01	0.31±.02	0.11±.02
HFW	0.41±.05	0.44±.05	0.59±.02	0.62±.02	<b>0.38±.02</b>	0.40±.01	0.47±.01	0.08±.02
ELW <sub>3</sub>	0.70±.04	0.51±.05	0.88±.02	0.91±.02	0.47±.03	<b>0.42±.02</b>	0.34±.02	0.03±.02
EFW <sub>3</sub>	0.17±.07	0.21±.06	0.22±.03	0.29±.04	0.79±.03	0.23±.05	<b>0.42±.02</b>	0.01±.02
NLB <sub>2,4</sub>	0.15±.10	0.25±.09	0.29±.07	0.40±.06	0.30±.03	0.01±.08	0.16±.09	<b>0.05±.02</b>

WWT<sub>d</sub> = direct effects for WWT; WWT<sub>m</sub> = maternal genetic effects for WWT;  $pe^2 = 0.04$ ,  $c^2 = 0.15$  for WWT;

NLB<sub>2,4</sub> represents average NLB across 2 to 4 year old records with  $r_g$  fixed at 0.999.

was also appropriate for NLB at two to five years of age. Accordingly, multiple-trait runs of adult with lamb and hogget traits were undertaken using EBW and EFW at three years of age. For NLB, two- to three-year-old records were each fitted simultaneously, assuming a constant genetic correlation of 0.999 among them (i.e. a “repeatability” model using a heterogeneous variance correlation structure, Gilmour, 1999). This was done because of the very different pattern of environmental correlations among weight traits and NLB, within and across years. A constant genetic correlation between each weight trait and NLB at each age was assumed for all models. The phenotypic correlation was estimated as the average of the correlations of the weight traits with each annual NLB expression.

### All traits

Parameter estimates coming from multiple trait runs involving adult traits, each including HBW in the model, are summarised in Table 3. On the basis of results presented in Table 2, maternal genetic effects were fitted for WWT only.

Genetic correlations of maternal WWT with later liveweights were lower than corresponding correlations of direct genetic effects on WWT with these other traits although this was not true for EFW or NLB. Genetic correlations among liveweight traits were higher than the corresponding phenotypic estimates; for HFW and EFW they were more similar. Genetic correlations of other traits with NLB were also greater than their phenotypic counterparts except for ELW for which both were close to zero. While genetic correlations of HBW (and later weights) with NLB were similar for each of the annual expressions of a ewe’s reproductive performance (0.35 to 0.45) and the corresponding phenotypic correlations were of similar magnitude, phenotypic correlations of HBW with NLB averaged across the first three lambings were much lower (0.10). This reflects the moderately strong positive environmental association of HBW (and ELW) with NLB within, but not across, years.

## DISCUSSION

Heritability estimates were in broad agreement with published values when due consideration is taken of the terms included in the analytical model (Fogarty, 1995). Probably the major exception is the high heritability estimate for 8-month autumn body weight compared with hogget body weight at 13 months, especially relative to that expected (approximately 0.3) from the proportional

development occurring between 8 and 12 months (11.3 kg average body weight gain), relative to that between weaning and 12 months (24.6 kg gain).

As judged from the small change in heritability estimates for EBW and EFW when HBW was fitted simultaneously, the effects of selection for HBW in one of the lines had little effects on the size of the within-line estimates, although phenotypic variances of later weight traits were increased.

Estimates of phenotypic and genetic correlations were also broadly similar to published estimates (Fogarty, 1995). Of particular relevance to improvement programmes for dual-purpose sheep is the relative size of the genetic correlations among traits affecting overall productivity. Few studies are able to a comparison of estimates coming from the same dataset.

All lamb and hogget traits had positive genetic correlations with adult wool and lamb production, the size of them increasing from weaning to 12 months of age. They were also lower in magnitude than the corresponding genetic correlations with ewe liveweight, implying a concomitant increase in feed costs beyond those associated with extra output, to early indirect (hogget) selection for improved meat and wool output.

Dual-purpose genetic response predictions for a selection index combining individual and maternal half-sib records (for WWT, ALW, HBW & HFW), paternal half-sib records (for the same traits), and dam records (for WWT and NLB) were derived to evaluate the relative contributions of the traits to economic progress using recently derived overall economic values for dual-purpose sheep (Amer, 2000). Despite its negative economic weighting, it predicted high responses in ELW, 87% of that expected from direct single trait selection for this trait alone. Responses in other traits were in line with those expected from earlier studies (e.g. Clarke and Rae, 1977; Johnson *et al.*, 1989). Restraining the response in ELW to zero required a ten-fold increase in the negative relative economic value for this trait, and reduced the correlation of the index with aggregate breeding merit from 0.68 to 0.37. Such restriction greatly increased the relative contribution of fleece weight to economic response, made little difference to the relative contribution of NLB, although the absolute rate of progress was nearly halved. It also greatly reduced the contribution of growth although maternal effects on weaning weight became relatively more important. These results indicate that current economic weights do not put high emphasis on reducing feed costs associated with increased mature

liveweight, and that there is a large reduction in and re-direction of expected selection response in output traits if concomitant increases in mature body size are to be avoided.

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