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Sex and age effects on genetic parameters for wool production and qualities

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ABSTRACT

Heritabilities and genetic correlations were estimated for New Zealand Romney sheep from within the selected and control lines of a 25-year selection experiment for greasy hogget fleece weight and yearling body weight. Average repeatability of clean fleece weight in 1 to 5 year-old ewes was 0.56, 25% higher than the average heritability of 0.44. The average genetic correlation among measurements at different ages was 0.89. Sexual dichotomy in the relative predictive power of hogget records was most apparent for greasy and clean fleece weights but was evident to some degree for bulk and brightness as well, due mainly to lower heritabilities in male compared to female hoggets. Average co-heritability of greasy hogget with adult clean fleece weights was 25% lower for male (0.26) compared to female (0.35) hoggets, in this case due to a lower genetic correlation (0.69 vs 0.81) as well as a lower heritability (0.33 vs 0.43, respectively). A repeatability model seemed an adequate approximation for estimation of breeding merit for most wool quality traits studied but not for lifetime wool production.

Keywords: genetic parameters; male and female hoggets; wool production and qualities.

INTRODUCTION

There is increasing evidence that genetic parameters of lifetime wool production vary with age and sex. Thus for Merinos, Atkins and Mortimer (1987), Atkins *et al.*, (1990) and Atkins (1990) showed that the heritability of adult fleece weight was significantly higher than the heritability of hogget fleece weight. While this was not found in the study of Hickson *et al.*, (1994), their results were in agreement that the genetic correlation between adult and hogget fleece weights was significantly less than unity, the pattern of genetic correlations being similar in both studies. Genetic correlation estimates for fibre diameter at different ages also suggested a need to separate adult from hogget expressions in defining breeding objectives, rather than using the traditional repeatability approach which assumes that all expressions are equally heritable and perfectly correlated genetically. Such an approach is also relevant to improvement of crossbred wools given both a lower heritability of fleece production and a lower average genetic correlation between hogget and adult records for male compared with female hoggets reported by Clarke *et al.*, (1995).

This study extends the results presented by Clarke *et al.*, (1995), to include data on additional animals and on additional traits that are indicative of genetic variations in wool quality.

MATERIALS AND METHODS

Experimental management, data collection and selection policies were described by Johnson *et al.*, (1995) and Morris *et al.*, (1996). Animals from all lines were shorn as lambs in December and as yearlings the following September/October. Breeding ewes were shorn each year in December. Heritabilities and genetic correlations were estimated from all three single trait selection and control lines rather than just the fleece weight and control lines studied

by Clarke *et al.*, (1995). Since pedigree linkages to common base parents were not available, within-line analyses were undertaken ignoring the genetic divergence that was developed among the lines by selection. Data were available on up to 6088 hoggets (3767 females and 2321 males) born and managed together from 1967 to 1988 (Clarke *et al.*, 1995). In 20 of these 21 birth years, most hogget fleeces were mid-side sampled for assessment of wool qualities. In 10 of the 14 years from 1977, 1137 animals were sampled for analysis of wool quality traits at 2, 3, 4 and/or 5 years of age, as described by Morris *et al.*, (1996).

Data were analysed by univariate and multivariate mixed-model REML methods fitting an animal model using ASREML (Gilmour, 1997). Fixed effects associated with year of birth and selection line within year of birth, fitted as an absorbed contemporary group (line x year subclasses), were included in the model. Effects associated with birth-rearing status, age of dam and date of birth accounted for little of the variation among animals (Morris *et al.*, 1996) and were excluded from the models from which parameters were estimated. Sex was included as part of the contemporary group definition for the more conventional analyses in which corresponding measurements on males and females were regarded as the same biological trait.

RESULTS

Adult Clean Fleece Weight

Estimates of genetic and phenotypic parameters of clean fleece weight measurements taken on hoggets and breeding ewes are presented in Table 1.

Heritability estimates were not significantly different among adjacent ages but tended to be lower at the two oldest ages than in younger animals. The average phenotypic correlation was 0.56, declining from 0.58 for adjacent annual phenotypic expressions, to 0.53 for records

TABLE 1: Estimates of phenotypic correlations (above diagonal), genetic correlations (below diagonal), heritabilities (h^2) and phenotypic variations (σ_p^2) from multivariate runs analysing all clean fleece weight measurements on females simultaneously

	fCh*	fC2	fC3	fC4	fC5	σ_p^2	h^2
fCh	-	0.53	0.55	0.51	0.47	0.17	0.49
		± 0.03	± 0.03	± 0.03	± 0.04		± 0.04
fC2	0.93	-	0.62	0.53	0.54	0.20	0.48
	± 0.06		± 0.03	± 0.03	± 0.04		± 0.06
fC3	0.89	0.90	-	0.60	0.63	0.32	0.51
	± 0.06	± 0.05		± 0.03	± 0.03		± 0.07
fC4	0.84	0.87	0.91	-	0.58	0.31	0.45
	± 0.09	± 0.08	± 0.08		± 0.05		± 0.08
fC5	0.83	0.85	0.96	0.96	-	0.29	0.33
	± 0.11	± 0.11	± 0.09	± 0.10			± 0.09

* Trait symbols: m/f=male/female; C=clean fleece weight; h/2...5=hogget/2...5 year-old

3 years apart, and to 0.47 for the smaller number of records on 1 and 5 year-old ewes (i.e. 4 years apart). The corresponding genetic correlations were all much higher and averaged 0.89, declining from 0.93 for records 1 year apart, to 0.85 for records 2 years apart and to 0.83 between 1 and 5 year-old records. Fitting a banded correlation model or a common genetic correlation among all measurements regardless of age, reduced the logarithm of the likelihood only slightly (from -11240.5 to -11241.7 for the pooled, common, correlation model), and gave similar heritability estimates at each age to those shown in Table 1. None of the individual genetic correlations presented in Table 1 were significantly different from the pooled estimate (0.92 \pm 0.04).

Relationships with Hogget Greasy Fleece Weight

Estimates of heritabilities of ewe and ram hogget greasy fleece weight and their genetic correlations with ewe clean fleece weights at each age are presented in Table 2.

TABLE 2: Estimates of phenotypic variance (σ_p^2), heritabilities (h^2 , bold) of greasy hogget fleece weight, and its genetic correlations with adult clean fleece weight from two multivariate runs analysing all fleece weight measurements simultaneously for hoggets of each sex.

Sex	h^2 (σ_p^2) Gh	Genetic correlations					Ave(2-5)
		fCh	fC2	fC3	fC4	fC5	
f	0.43 ± 0.03 ($\sigma_p^2=0.23$)	0.95 ± 0.01	0.79 ± 0.06	0.77 ± 0.07	0.84 ± 0.08	0.82 ± 0.10	0.81
				Average co-heritability			0.35
m	0.33 ± 0.04 ($\sigma_p^2=0.32$)	0.89 ± 0.06	0.73 ± 0.09	0.65 ± 0.10	0.76 ± 0.11	0.63 ± 0.15	0.69
				Average co-heritability			0.26

* Trait symbols: m/f=male/female; G/C=greasy/cleanfleece weight; h/2...5=hogget/2...5 year-old

Heritability of greasy fleece weight was significantly lower in ram (0.33 \pm 0.04) compared with ewe hoggets (0.43 \pm 0.03). The genetic correlations with clean fleece weight records on the ewes were also consistently lower for each ewe record in ram hoggets (average 0.69) than in ewe hoggets (average 0.81), and both were lower than the average genetic correlation among all clean fleece weight records of the ewes (0.89, Table 1). The pattern of genetic correlations among breeding ewe records was similar for the ram and ewe analyses.

Also shown in Table 1 are the average co-

heritabilities calculated as the product of the average genetic correlation (2 to 5 year-olds) with the geometric mean of the hogget and the average of the 2 to 5 year-old heritability estimates (from Table 1). It indicates the predictive accuracy of the hogget record. On average it was 25% lower for male compared with female hoggets (0.69 versus 0.81). An even greater sex disparity was found in co-heritabilities for predicting adult clean fleece weight records from ram (0.21) compared with ewe hogget (0.39) clean fleece weights (details not reported).

Sex and Age Relationships among Wool Quality Traits

Because of the smaller number of animals measured for wool quality indicators, results are summarised as the genetic correlations of hogget with adult measurements for analyses undertaken separately for each adult age and each sex of hogget (Table 3). For the production traits, for which greater numbers of records were available, this approach gave similar conclusions to the combined multivariate analyses of all traits (Tables 1 and 2, above).

TABLE 3: Estimates of heritabilities (h^2 , bold) and genetic correlations ($r_{g \pm se}$) of hogget with breeding ewe fleece qualities (σ_p^2 in brackets).

Trait	Sex	h^2	Hoggets				Breeding ewes	
			2 year	3 year	4 year	5 year	Ave (2-5)	
SL	f	h^2	0.43 ± 0.04	0.28 ± 0.04	0.34 ± 0.04	0.23 ± 0.05	0.35 ± 0.06	0.30
		r_g		0.80 ± 0.06	0.76 ± 0.07	0.69 ± 0.09	0.62 ± 0.09	0.72
		σ_p^2	(3.1)	(3.3)	(4.0)	(3.7)	(3.7)	(3.7)
			Ave co-heritability :					0.26
m	h^2 /rg	h^2 /rg	0.35 ± 0.05	0.92 ± 0.09	0.81 ± 0.10	0.79 ± 0.14	0.67 ± 0.12	0.80
		σ_p^2	(2.5)					
				Ave co-heritability :				
FD	f	h^2	0.42 ± 0.04	0.54 ± 0.08	0.55 ± 0.07	0.49 ± 0.10	0.57 ± 0.11	0.54
		r_g		0.87 ± 0.06	0.76 ± 0.08	0.75 ± 0.09	0.85 ± 0.09	0.81
		σ_p^2	(5.7)	(6.3)	(7.9)	(7.8)	(7.4)	
			Ave co-heritability :					0.39
m	h^2 /rg	h^2 /rg	0.40 ± 0.05	1.06 ± 0.10	0.95 ± 0.09	0.88 ± 0.11	0.93 ± 0.12	0.96
		σ_p^2	(6.4)					
				Ave co-heritability :				
FDSD	f	h^2	0.34 ± 0.07	0.47 ± 0.09	0.42 ± 0.10	0.55 ± 0.11	0.82 ± 0.11	0.57
		r_g		0.95 ± 0.06	0.95 ± 0.07	0.81 ± 0.09	0.79 ± 0.09	0.88
		σ_p^2	(0.71)	(0.80)	(1.06)	(0.91)	(1.03)	
			Ave co-heritability :					0.39
m	h^2 /rg	h^2 /rg	0.42 ± 0.08	0.88 ± 0.13	0.91 ± 0.12	0.79 ± 0.14	0.76 ± 0.14	0.80
		σ_p^2	(0.66)					
				Ave co-heritability :				
Bulk	f	h^2	0.62 ± 0.07	0.70 ± 0.12	0.62 ± 0.13	0.35 ± 0.14	0.33 ± 0.14	0.50
		r_g		0.87 ± 0.07	0.77 ± 0.10	0.94 ± 0.15	1.17 ± 0.16	0.94
		σ_p^2	(8.2)	(23)	(13)	(11)	(11)	
			Ave co-heritability :					0.52
m	h^2 /rg	h^2 /rg	0.45 ± 0.08	1.03 ± 0.10	0.78 ± 0.15	0.87 ± 0.25	1.15 ± 0.31	0.96
		σ_p^2	(8.5)					
				Ave co-heritability :				
Y	f	h^2	0.36 ± 0.08	0.23 ± 0.08	0.17 ± 0.09	0.40 ± 0.11	0.10 ± 0.13	0.23
		r_g		0.74 ± 0.18	0.96 ± 0.23	0.91 ± 0.13	0.84 ± 0.57	0.86
		σ_p^2	(6.5)	(4.8)	(5.5)	(6.0)	(6.4)	
			Ave co-heritability :					0.25
m	h^2 /rg	h^2 /rg	0.18 ± 0.08	0.87 ± 0.25	1.27 ± 0.34	0.82 ± 0.21	1.27 ± 0.56	1.06
		σ_p^2	(6.5)					
				Ave co-heritability :				
Y-Z	f	h^2	0.23 ± 0.07	0.17 ± 0.08	0.14 ± 0.09	0.29 ± 0.10	0.17 ± 0.12	0.19
		r_g		0.50 ± 0.26	0.64 ± 0.31	0.75 ± 0.20	0.68 ± 0.36	0.64
		σ_p^2	(2.1)	(3.0)	(3.9)	(3.0)	(2.4)	
			Ave co-heritability :					0.13
m	h^2 /rg	h^2 /rg	0.24 ± 0.08	0.55 ± 0.31	0.75 ± 0.33	0.97 ± 0.29	0.49 ± 0.43	0.69
		σ_p^2	(2.4)					
				Ave co-heritability :				

Trait abbreviations: SL = staple length; FD = fibre diameter; FDSD = fibre diam. std. devn.; Y = brightness; Y-Z = yellowness

Heritability estimates for ewe hoggets were higher than the average of the estimates for breeding ewes, for all traits other than fibre diameter (both mean and variability of fibre diameter). This is in contrast to the estimates presented by Morris *et al.*, (1996), which were not derived from a combined multivariate analysis of hogget and adult measurements together in the same model. There was little evidence of age trends among the breeding ewes, with the exception of bulk whose heritability tended to decline with age of adult, and staple length for which the genetic correlation with the hogget measurement tended to decline with age for both ram and ewe hoggets. Highest genetic correlations of hogget with adult measurements (0.9 or greater when averaged across both sexes) were observed for bulk (both sexes), brightness and fibre diameter (especially males); they were on average lowest for staple length (0.76) and yellowness (0.67). Co-heritabilities were remarkably similar in males and females: identical for staple length and fibre diameter variability, 13% higher in females for bulk and yellowness, and 13% lower in females for fibre diameter and brightness.

TABLE 4: Estimates of heritabilities (diagonal, bold) and genetic correlations among hogget measurements on each sex (refer earlier tables for phenotypic standard deviations)

Female	GFW	CFW	SL	FD	FSDS	Bulk	Y	Y-Z
GFW	0.42							
	±.04							
CFW	0.96	0.47						
	±.01	±.04						
SL	0.40	0.54	0.43					
	±.06	±.05	±.04					
FD	0.52	0.55	0.54	0.42				
	±.06	±.05	±.06	±.03				
FSDS	0.26	0.27	0.04	0.00	0.36			
	±.13	±.13	±.15	±.15	±.05			
Bulk	-0.09	-0.32	-0.68	-0.08	0.00	0.65		
	±.11	±.10	±.08	±.11	±.14	±.07		
Y	0.03	0.05	-0.03	-0.20	-0.05	0.03	0.37	
	±.14	±.14	±.15	±.14	±.17	±.14	±.08	
Y-Z	0.20	0.10	0.25	0.42	0.33	0.06	-0.49	0.26
	±.15	±.15	±.18	±.16	±.19	±.17	±.15	±.07
Male	GFW	CFW	SL	FD	FSDS	Bulk	Y	Y-Z
GFW	0.35							
	±.05							
CFW	0.96	0.36						
	±.01	±.05						
SL	0.48	0.63	0.37					
	±.08	±.07	±.15					
FD	0.57	0.59	0.51	0.38				
	±.08	±.07	±.09	±.05				
FSDS	0.47	0.51	0.08	0.17	0.42			
	±.13	±.14	±.19	±.16	±.08			
Bulk	0.00	-0.19	-0.03	0.14	0.09	0.52		
	±.14	±.14	±.19	±.16	±.17	±.08		
Y	0.00	-0.14	-0.05	-0.05	0.11	0.21	0.18	
	±.21	±.23	±.26	±.22	±.25	±.22	±.08	
Y-Z	0.58	0.46	0.37	0.44	0.60	0.32	-0.56	0.27
	±.15	±.16	±.20	±.17	±.18	±.21	±.23	±.07
Across-sex	GFW	CFW	SL	FD	FSDS	Bulk	Y	Y-Z
	1.01	1.01	0.99	1.01	1.06	0.90	0.77	1.07
correls.	±.06	±.06	±.06	±.05	±.09	±.07	±.21	±.15

Trait abbreviations: GFW = greasy fleece weight; CFW = clean fleece weight; SL = staple length; FD = fibre diameter; FSDS = fibre diam. std. devn.; Y = brightness; Y-Z = yellowness

Correlations among Hogget Records

These are presented separately for each sex in Table 4, along with the genetic correlations among corresponding measurements in each sex. The estimates involving clean fleece weight (CFW) and greasy fleece weight (GFW) came from multivariate analyses fitting, for both ewe and ram hoggets simultaneously, GFW (or CFW for correlations with this trait), together with each wool quality trait. Covariances among wool quality traits were from multivariate runs fitting GFW together with each pair of quality traits, in separate runs for hoggets of each sex.

Heritabilities were higher in females than in males for staple length, fibre diameter, brightness and bulk. Genetic correlations across the two sexes showed a tendency to depart from unity for brightness and bulk only. Genetic correlations among traits for each sex were similar apart from some of those involving fibre diameter variation, bulk and yellowness. The genetic associations of both fibre diameter variation and yellowness with fleece weight were more highly positive in males than in females, as were, to a lesser extent, those for yellowness with fibre diameter variation and bulk. Bulk showed a negative association with staple length in females but not in males where the genetic correlation was not significantly different from zero.

DISCUSSION

Genetic parameters for ewe clean fleece weight records showed a similar pattern to those presented previously by Clarke *et al.*, (1995) for just two of the three selection lines studied here, the average heritability estimate for 1 to 5 year-old records being 0.44. This was 20 % lower than the average repeatability of clean fleece weight records (0.56), suggesting that permanent environmental effects may also be important to repeated expressions of an animal's fleece production. No significant age pattern was apparent among estimates of the genetic correlation among fleece weights taken at different ages. The genetic correlation averaged approximately 0.9, significantly less than unity in line with other recent results (e.g. Hickson *et al.*, 1994).

Sex differences in the predictive power of hogget records were most apparent for greasy and clean fleece weights for which greatest information was available. Average co-heritability of greasy hogget fleece weight with 1 to 5 year-old female clean fleece weight records was 0.37 for ewe hoggets and 0.28 for ram hoggets, the latter being higher than published previously for just two of the three selection lines (0.21). Thus the relative genetic predictive power for lifetime clean wool production was 23% lower for ram hogget greasy fleece weights compared to ewe hogget greasy fleece weights.

For hogget wool quality traits, heritabilities tended to be at least 20% lower in male than in female hoggets for brightness, bulk and staple length. Highest heritabilities and genetic correlations were observed for bulk. Co-heritabilities of hogget with older female records (Table 3), were highest for bulk, fibre diameter and fibre diameter variation and lowest for yellowness, brightness and staple length.

The averages of the parameter estimates reported for each sex were generally similar to the estimates for both sexes together and reported by Morris *et al.*, (1996). The major exceptions were for traits showing evidence of different genetic correlations in rams and ewes. One of the most notable was the lower genetic antagonism of bulk with staple length in male compared with female hoggets. Taking account of their standard errors, the genetic correlations reported are also similar to those published by Wuliji *et al.*, (1998). The major differences were their lower genetic correlations of fibre diameter and yellowness with clean fleece weight and staple length.

Overall, results indicate that sexual dichotomy in the predictive power of hogget records was most apparent for greasy and clean fleece weight and to some degree also for brightness and bulk. Lifetime adult wool production in mixed-age flocks of commercial ewes is probably better regarded as a "sex-limited" trait, since little in the way of economic reward comes from males. Such an approach would focus genetic improvement issues more clearly on the accuracy of early indicators of lifetime female performance, whether these be measurements taken on young females or on young males among which the intensity of selection can be much higher, and on the use of information on relatives of the same or of different sex. Nevertheless, the derived co-heritability estimates suggest that while a repeatability model could be adequate for most wool quality traits studied, it is less adequate for lifetime clean wool production.

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