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A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep

E. Safari, N.M. Fogarty*, A.R. Gilmour

The Australian Sheep Industry Cooperative Research Centre, NSW Department of Primary Industries, Orange Agricultural Institute, Forest Road, Orange NSW 2800, Australia

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Abstract

Genetic parameters for a range of sheep production traits have been reviewed from estimates published over the last decade. Weighted means and standard errors of estimates of direct and maternal heritability, common environmental effects and the correlation between direct and maternal effects are presented for various growth, carcass and meat, wool, reproduction, disease resistance and feed intake traits. Weighted means and confidence intervals for the genetic and phenotypic correlations between these traits are also presented. A random effects model that incorporated between and within study variance components was used to obtain the weighted means and variances. The weighted mean heritability estimates for the major wool traits (clean fleece weight, fibre diameter and staple length) and all the growth traits were based on more than 20 independent estimates, with the other wool traits based on more than 10 independent estimates. The mean heritability estimates for the carcass and meat traits were based on very few estimates except for fat (27) and muscle depth (11) in live animals. There were more than 10 independent estimates of heritability for most reproduction traits and for worm resistance, but few estimates for other sheep disease traits or feed intake. The mean genetic and phenotypic correlations were based on considerably smaller numbers of independent estimates. There were a reasonable number of estimates of genetic correlations among most of the wool and growth traits, although there were few estimates for the wool quality traits and among the reproduction traits. Estimates of genetic correlations between the groups of different production traits were very sparse. The mean genetic correlations generally had wide confidence intervals reflecting the large variation between estimates and relatively small data sets (number of sires) used. More accurate estimates of genetic parameters and in particular correlations between economically important traits are required for accurate genetic evaluation and development of breeding objectives.

Keywords: Heritability; Genetic correlations; Genetic models; Maternal effects

1. Introduction

Breeding objectives for sheep enterprises are becoming more complex. The increasing economic

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* Corresponding author. Tel.: +61 2 6391 3813; fax: +61 2 6391 3922.

E-mail address: neal.fogarty@agric.nsw.gov.au (N.M. Fogarty).

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value of meat relative to wool and increased importance of lamb and sheepmeat production from Merino wool producing flocks in recent years (Banks, 2002) means that more traits are contributing to the overall objective and profit of many sheep enterprises. The increased value of meat also enhances the importance of reproduction traits, both in Merino and maternal meat breeds. The inclusion of disease resistance (Eady et al., 2003) and quality traits for both wool (Mortimer and Atkins, 1993; Brown et al., 2002) and meat (Fogarty et al., 2003) are also being advocated along with feed intake (Lee et al., 2002) and behaviour traits that affect production (Lambe et al., 2001).

Development of effective genetic evaluation and improvement programmes requires knowledge of the genetic parameters (genetic variance of each trait and covariances among traits) for these economically important production traits. Accurate estimation of these genetic parameters and in particular genetic correlations requires large across-generation data sets for each relevant population which are not always available. Pooling estimates from several populations may provide more reliable parameter estimates than those obtained from a single population if there is stability across populations.

Genetic parameters for sheep production traits were reviewed by Fogarty (1995) who reported weighted means of estimates of heritability and genetic and phenotypic correlations from the literature. During the last decade or so, there has been extensive development of statistical procedures and software for estimation of variance components. The animal mixed model using REML procedures is now used extensively for analysis of data with Bayesian procedures also used in some instances. The availability of larger across-generation data sets from both field data and research resource flocks, the advances in computing capacity and development of software packages applying animal models have all resulted in publication of a plethora of what are expected to be better estimates of genetic parameters for sheep production traits. These advances in procedures have also allowed estimation of additional variance components such as maternal heritability, permanent environmental effects and the correlation between direct and maternal genetic effects for many traits.

Genetic parameter estimates for a comprehensive range of sheep production traits have recently been compiled by Safari and Fogarty (2003) from the literature over the last decade. The current study analyses and presents a summary and critical review of those published genetic parameter estimates and highlights the traits where further research is required. In addition, relevant methodology, models and data structures for genetic parameter estimation and future analysis of data are examined.

2. Materials and methods

2.1. Scope and traits

This review is based on estimates of the genetic parameters and the information relating to the study size and scope from 165 studies in sheep that were compiled by Safari and Fogarty (2003). The literature reports covered the period from approximately 1992 to 2003 and the estimates were generally derived from mixed model REML procedures, with some Bayesian estimates also included. The focus is on traits that are important to wool and sheepmeat production systems and excluded milk production. The traits covered in this review represent seven broad categories: growth, carcass, meat, wool, reproduction, disease resistance and feed intake.

Growth traits were defined as weight at various ages: birth weight (BW), weaning weight (WW, 3–5 months of age), post-weaning weight (PWW, up to 12 months of age), adult weight (AW, >12 months of age) and growth rate (G/D). Wool traits included greasy fleece weight (GFW), clean fleece weight (CFW), mean fibre diameter (FD), coefficient of variation (CVFD) and standard deviation of fibre diameter (SDFD), staple length (SL), staple strength (SS), yield (YLD) and crimp frequency. The heritability estimates were classified by breed type (wool, dual-purpose and meat breeds) for some traits where there was enough information.

Carcass traits included fat and muscle measurements on live animals using ultrasound devices and on carcasses. Most fat measurements on live sheep were at the C site, over the eye muscle (*m. longissimus lumborum*) at about the 12th rib (FATl). Fat measurements adjusted for liveweight (FATla) were also included. Carcass fat measurements were at the C site (FATC) or at the GR site (FATGR), which is total soft tissue depth over the 12th rib, 110 mm from the midline. Muscle measurements were generally for the eye muscle at the 12th rib, with the cross-section dimensions depth (EMD) and width (EMW) and area (EMA) reported for carcasses and similar measurements in live animals (EMDl, EMWl and EMAl, respectively). Estimates for carcass weight (CW), dressing yield (DY), conformation (CONF), meat pH, meat colour and the amount of lean (LMY) were also included.

The reproduction traits included the number of lambs born (NLB), number of lambs weaned (NLW) and weight of lamb weaned (WW) per ewe joined (/EJ) and per ewe lambing (/EL). Estimates were also presented for the components of reproduction: number of lambs born per ewe lambing (or litter size—NLB/EL), fertility (lambed or not—EL/EJ), ewe rearing ability (NLW/NLB), lamb survival, embryo survival and ovulation rate, as well as the male trait scrotal circumference.

Disease resistance traits were worm resistance, measured as faecal egg count (FEC) and fleece rot incidence and severity. Feed intake traits were digestible organic matter intake (FI) and efficiency of wool growth (g/kg FI).

2.2. Analysis and presentation of results

The data set compiled by Safari and Fogarty (2003) from the literature included direct and maternal heritability, common environmental effects as a proportion of the total variance, correlation between direct and maternal genetic effects for the various traits as well as the genetic and phenotypic correlations between traits and standard errors of estimates where they were included in the original report. Information was also included on the data structure, including the number of records, number of sires and dams, number of years of data and the mean and coefficient of variation for each trait. That data set is the basis for the information presented in this paper. Where parameter estimates in different publications were identified as being derived from the same or similar data only one report, generally the most recent, was included in this analysis. Parameter estimates from data with less than 20 sires were also excluded.

Weighted means for direct and maternal heritability, common environmental effects and the correlation between direct and maternal genetic effects as well as the coefficient of variation are presented for the various traits. Since we are combining information from separate studies there are two types of variance to be considered—within and between studies. The within study variance reflects how accurately the parameter is estimated for that study and relates to the size of the study. The between study component allows for the fact that the parameters are drawn from different sub-populations and provides a test of our assumption that parameters are stable across populations. The weighted means need to be formed recognising both sources of variation. Since not all studies reported the within study variance for the parameter estimates, three different procedures were evaluated to estimate it as a basis for forming the weighted means for the heritability estimates: (i) the reported variance where available and a predicted value otherwise, (ii) the estimated theoretical variance and (iii) a variance proportional to the inverse of the number of records. For (i), the standard error was predicted when none was reported as follows. First, a weighted mean standard deviation ($\mathrm{SD_W}$) was obtained from the reported standard errors by the combined variance method (Sutton et al., 2000) using Eq. (1), where s_i is the standard error and n_i is the number of records for the ith estimate (i=1, 2, ..., y). The predicted standard error for estimates with no reported standard error was then calculated by dividing $\mathrm{SD_W}$ by the square root of the number of records in the estimate.

$$\mathrm{SD_W} = \left[\frac{\sum_{i=1}^{y} s_i^2 n_i^2}{\sum_{i=1}^{y} n_i}\right]^{0.5} \tag{1}$$

For procedure (ii), the theoretical standard error for an estimate of heritability was obtained using Eq. (2) from Falconer and Mackay (1996) where t is the intraclass correlation, approximated by $h^2/4$, k is the average number of offspring per sire and s is the number of sires.

$$se_{\hat{h}_2} = 4\left[\frac{2(1-t)^2[1+(k-1)t]^2}{k(k-1)(s-1)}\right]^{0.5} \tag{2}$$

The three different methods resulted in very similar weighted means of heritability and only results based on the number of records (procedure iii) are presented here. The variance proportional to the inverse of the number of records (procedure iii) was also used for the within study variance for maternal heritability, common environmental effects, correlation between direct and maternal genetic effects and the coefficient of variation, because the number of records was available for all studies.

The phenotypic and genetic correlations were transformed to an approximate normal scale to remove the dependency of the variance on the estimate, using Fisher's Z transformation (Steel and Torrie, 1960) in Eq. (3) with the standard error from Eq. (4), where r is the correlation (phenotypic or genetic) and n is the number of records (phenotypic correlation) or the number of sires (genetic correlation). The weighted mean of the Z transformed correlations was calculated and back transformed using Eq. (5), where r_w is the weighted mean correlation (phenotypic or genetic) and z is the weighted mean for the Z transformed correlations.

$$Z = 0.5\log\left[\frac{1+r}{1-r}\right] \tag{3}$$

$$se_Z = (n-3)^{-0.5} \tag{4}$$

$$r_w = \frac{e^{2z}-1}{e^{2z}+1} \tag{5}$$

The results showed that the generated standard errors using Eq. (4) were highly correlated with those in studies that reported standard errors for genetic correlations. Similar procedures were previously used by Koots et al. (1994b) to obtain weighted estimates of correlations in beef production traits.

The ASREML program (Gilmour et al., 2002) was used to obtain the weighted means for parameter estimates using a random effects model incorporating both components of variance. The model allowed estimates to represent random subpopulations with differing parameters drawn from the overall population. This took into account the extra variation implied in this assumption by including between study and within study components of variance and used Residual Maximum Likelihood to determine the relative contributions of the between and within variances to the weights. The model is shown in Eq. (6), where θ_i is the estimate of a parameter in the ith study, μ is the population mean (weighted mean of the estimates), s_i is the between study component of the deviation from the mean and e_i is the within study component due to sampling error in the ith estimate. The components s_i and e_i are normally distributed with mean zero and variances σ_s^2 and V, respectively. For direct and maternal heritability, common environmental effects, correlation between direct and maternal genetic effects and the coefficient of variation, $V=\sigma_e^2/n_i$ where n_i is the number of records. For the correlations $V=\sigma_e^2/(n_i-3)$, where n_i is the number of records for the phenotypic correlations and the number of sires for the genetic correlations. The standard errors for the weighted means and the 95% confidence intervals for the correlations were derived from V, with those for correlations being back transformed using Eq. (5).

$$\theta_i = \mu + s_i + e_i \tag{6}$$

3. Results and discussion

3.1. Heritability and coefficient of variation

3.1.1. Growth traits

The weighted means of heritability for growth traits were generally moderate in magnitude and ranged from 0.15 to 0.41 with very low standard errors (range 0.01–0.04) of the means (Table 1). The mean heritabilities for weight at birth and weaning were similar and heritability increased with age to post weaning and adult weights. There was a tendency for the mean heritabilities to be higher for the wool breeds than for dual-purpose and meat breeds at all ages. The mean heritabilities found in this study, including the trends for age and among breeds, were generally similar to those found by Fogarty (1995). The only large discrepancies were among the wool breeds in which the mean heritabilities in this study were higher for birth weight (0.21±0.03 vs. 0.13±0.04) and lower for weaning weight (0.23±0.02 vs. 0.33±0.03) and adult weight (0.41±0.02 vs. 0.57±0.05) and also

Table 1
Number of literature estimates (n) and weighted mean (±S.E.) for heritability (h^2) and coefficient of variation (CV) for growth, carcass and meat traits with the corresponding values from Fogarty (1995)

Trait	Heritability				Coefficient of variation		
	This study		Fogarty (1995)		This study		Fogarty (1995)
	n	h^2±S.E.	n	h^2±S.E.	n	CV±S.E.	CV
Growth							
Birth weight[a]	8	0.21±0.03	6	0.13±0.04	4	14.2±1.5	17
Birth weight[b]	26	0.19±0.02	19	0.19±0.02	23	16.5±0.6	
Birth weight[c]	6	0.15±0.02	7	0.12±0.05	6	19.2±1.0	
Weaning weight[a]	15	0.23±0.02	9	0.33±0.03	9	15.8±1.5	15
Weaning weight[b]	40	0.18±0.02	42	0.20±0.01	36	15.9±0.4	
Weaning weight[c]	7	0.18±0.04	13	0.21±0.05	7	18.0±0.7	
Post-weaning weight[a]	18	0.33±0.02	–	–	13	12.8±1.2	13
Post-weaning weight[b]	23	0.29±0.03	26	0.26±0.02	21	12.4±0.6	
Post-weaning weight[c]	9	0.21±0.01	15	0.28±0.02	9	10.6±1.8	
Adult weight[a]	27	0.41±0.02	19	0.57±0.05	19	12.4±0.7	10
Adult weight[b]	19	0.31±0.03	29	0.31±0.03	18	10.6±1.0	
Adult weight[c]	4	0.30±0.03	5	0.25±0.05	4	6.0±1.0	
Daily gain	21	0.17±0.01	–	–	19	19.8±1.5	–
Carcass							
Carcass weight	4	0.20±0.06	–	–	4	17.6±1.5	–
Dressing yield (%)	3	0.42±0.05	–	–	3	46.7±0.9	–
Conformation	4	0.29±0.02	–	–	4	17.7±4.9	–
Fat depth—live	27	0.26±0.02	30	0.28±0.02	26	20.4±2.1	30
Fat depth—live, adj. wt.	18	0.25±0.02	22	0.26±0.03	17	12.7±2.0	–
Fat depth—carcass (C site)	6	0.30±0.03	24	0.31±0.02	6	46.2±4.9	36
Fat depth—carcass (GR site)	3	0.32±0.04	–	–	3	40.1±3.5	–
Eye muscle depth (EMD)—live	11	0.24±0.03	20	0.24±0.04	11	9.8±0.6	11
Eye muscle width (EMW)—live	4	0.06±0.01	–	–	4	8.8±0.3	–
Eye muscle area (EMA)—live	3	0.12±0.02	–	–	3	8.2±0.5	–
EMD—live, adj. wt.	5	0.22±0.04	11	0.29±0.02	5	10.8±1.3	–
EMW—live, adj. wt.	3	0.04±0.03	–	–	3	7.3±0.3	–
EMA—live, adj. wt.	3	0.14±0.01	–	–	3	6.9±0.2	–
EMD—carcass	4	0.30±0.03	18	0.29±0.02	4	11.0±0.9	11
EMW—carcass	4	0.38±0.10	–	–	4	6.9±0.4	–
EMA—carcass	5	0.41±0.07	–	–	5	13.8±1.9	–
Meat							
Lean meat yield (LMY)	2	0.35±0.02	–	–	2	9.0±4.0	–
Meat pH	2	0.18±0.01	–	–	2	6.0±1.0	–
Meat colour $L*$	2	0.16±0.03	–	–	2	9.5±0.5	–
Meat colour $a*$	2	0.04±0.03	–	–	2	16.0±0.0	–
Meat colour $b*$	2	0.05±0.01	–	–	2	21.0±1.0	–

[a] Wool breeds.

[b] Dual-purpose breeds.

[c] Meat breeds.

lower for post weaning weight among meat breeds (0.21±0.01 vs. 0.28±0.02). In contrast to the trend for heritabilities, there was a slight decline in the weighted mean coefficient of variation with age from birth to adult, which was also reported by Fogarty (1995). The mean coefficient of variation was greater among meat breeds than dual-purpose and wool breeds for birth and weaning weight, but this trend was reversed for post weaning and adult weights.

3.1.2. Carcass and meat traits

The weighted mean heritabilities for fat depth (Table 1) were slightly higher in carcasses (0.30±0.03 at the C site and 0.32±0.04 at the GR site) than in live animals (0.26±0.02), which were similar to the means in Fogarty (1995). Adjustment of live fat depth for live weight did not affect the heritability, but considerably reduced the coefficient of variation. The mean coefficients of variation for fat depth in the carcass were more than double that in live animals.

Carcass eye muscle measurements had moderate to high weighted mean heritabilities (depth 0.30±0.03, width 0.38±0.10 and area 0.41±0.07). These means were based on 4 or 5 estimates and were slightly higher than the weighted mean of 0.29±0.02 reported by Fogarty (1995) from 18 estimates. The heritabilities for eye muscle measurements in live animals were generally lower than the same measures in carcasses. In contrast to measurements in carcasses, the mean heritability for eye muscle depth (0.24±0.03) was considerably higher than width (0.06±0.01) in live animals, which reflects the poorer accuracy of measurement of width using ultrasound. There was little effect on the mean heritabilities or coefficients of variation from adjustment of the live muscle measurements for weight. The majority of estimates for fat and muscle dimensions were obtained using a simple additive model. Recent studies in live animals have reported maternal effects ranging from 0.04 to 0.08 for fat depth and 0.03 to 0.16 for muscle depth as well as significant permanent environment effects in some cases (Larsgard and Olesen, 1998; Maniatis and Pollott, 2002a; Simm et al., 2002; Clarke et al., 2003), which suggests that these effects need to be included in the models for estimation of these parameters.

The mean heritabilities for lean meat yield (0.35±0.02), dressing yield (0.42±0.05) and carcass conformation (0.29±0.02) were moderate to high and similar to those for carcass muscle measurements. The indicator traits for meat quality had moderate mean heritabilities for meat pH (0.18±0.01) and meat colour (L^* brightness 0.16±0.03), whereas those for other meat colour measurements were low (a^* redness 0.04±0.03, b^* yellowness 0.05±0.01). It should be noted that the mean heritabilities for these meat quality indicator traits are based on only two small studies.

3.1.3. Wool traits

The weighted mean heritabilities for greasy fleece weight in both wool (0.37±0.02) and dual-purpose breeds (0.38±0.03) and clean fleece weight in wool breeds (0.36±0.02) were each based on at least 20 estimates (Table 2) and were all similar and very close to those means reported by Fogarty (1995). In contrast the mean for clean fleece weight in dual-purpose breeds (0.51±0.07), based on only 6 estimates, was considerably higher than these other means and also higher than that reported by Fogarty (1995) from 15 estimates (0.34±0.04). Three of the 6 studies reported heritability estimates of at least 0.6 in Whiteface (Saboulard et al., 1995), Afrino (Snyman et al., 1995) and South African Meat Merino (Cloete et al., 2001) breeds, which were not included in Fogarty (1995). Snyman et al. (1995) attributed their high heritability to large variance in clean fleece weight due to a lack of selection in the Afrino flock, which is also reflected in the high coefficient of variation for clean fleece weight in dual-purpose breeds. Mean heritabilities for fibre diameter (0.59±0.02), coefficient of variation of fibre diameter (0.52±0.04), yield (0.56±0.03) and staple length (0.46±0.04) in wool breeds were very high and similar to those in dual-purpose breeds. The mean heritabilities for fibre diameter were slightly higher than those reported by Fogarty (1995) in both wool and dual-purpose breeds (0.51±0.03 and 0.52±0.03, respectively).

The coefficients of variation for fleece weight were approximately 16% and yield and fibre diameter approximately 7%, with little difference between wool and dual-purpose breeds except for clean fleece weight in dual-purpose breeds as discussed above. The coefficient of variation for staple strength was higher (29%), with the other wool traits ranging from 12% to 16%.

3.1.4. Reproduction traits

Weighted mean heritabilities for reproduction traits were generally low (Table 2). The means for number of lambs born (0.10±0.01), number of lambs weaned (0.07±0.01) and weight weaned (0.13±0.03), all per ewe joined and for the same traits per ewe lambing (0.13±0.01, 0.05±0.01 and 0.11±0.02, respectively) as well as ewe fertility (0.08±0.01), ewe rearing ability (0.06±0.02) and lamb survival (0.03±0.01)

Table 2
Number of literature estimates (*n*) and weighted mean (±S.E.) for heritability (h^2) and coefficient of variation (CV) for wool and reproduction traits with the corresponding values from Fogarty (1995)

Trait	Heritability				Coefficient of variation		
	This study		Fogarty (1995)		This study		Fogarty (1995)
	n	h^2±S.E.	*n*	h^2±S.E.	*n*	CV±S.E.	CV
Wool							
Greasy fleece weight[a]	20	0.37±0.02	25	0.34±0.03	10	16.5±1.1	15
Greasy fleece weight[b]	22	0.38±0.03	51	0.36±0.03	20	16.2±0.6	15
Clean fleece weight[a]	30	0.36±0.02	28	0.37±0.03	20	16.2±0.5	15
Clean fleece weight[b]	6	0.51±0.07	15	0.34±0.04	3	20.8±2.8	–
Fibre diameter (FD)[a]	33	0.59±0.02	27	0.51±0.03	19	7.4±0.3	8
Fibre diameter (FD)[b]	8	0.57±0.05	16	0.52±0.03	5	7.2±0.5	–
Coefficient of variation of FD	14	0.52±0.04	–	–	9	12.2±0.3	–
Standard deviation of FD	5	0.52±0.05	–	–	3	14.7±1.2	–
Staple length[a]	15	0.46±0.04	–	–	8	11.9±0.7	–
Staple length[b]	6	0.48±0.03	–	–	5	14.0±1.0	–
Staple strength	11	0.34±0.03	–	–	5	29.2±2.5	–
Yield[a]	15	0.56±0.03	–	–	8	7.0±0.2	–
Yield[b]	3	0.48±0.04	–	–	1	6.0	–
Crimp frequency	6	0.41±0.03	–	–	9	16.1±1.4	–
Reproduction							
Lambs weaned/ewe joined	11	0.07±0.01	18	0.05±0.01	8	63.5±4.2	73
Lambs born/ewe joined	19	0.10±0.01	22	0.08±0.02	12	52.7±2.6	58
Weight weaned/ewe joined	7	0.13±0.03	4	0.13±0.06	7	48.4±7.3	43
Lambs weaned/ewe lambing	8	0.05±0.01	25	0.05±0.01	7	45.0±1.4	51
Lambs born/ewe lambing	49	0.13±0.01	53	0.10±0.01	30	34.1±0.6	36
Lambs born alive/ewe lambing	2	0.10±0.05	–	–	2	38.5±1.5	–
Weight weaned/ewe lambing	11	0.11±0.02	8	0.14±0.02	8	35.6±2.8	51
Ewes lambing/ewe joined (fertility)	18	0.08±0.01	18	0.06±0.02	15	51.5±4.9	47
Ewe rearing ability	7	0.06±0.02	12	0.07±0.02	6	40.1±2.9	–
Lamb survival	16	0.03±0.01	24	0.04±0.01	3	47.0±5.8	46
Embryo survival	4	0.01±0.01	–	–	4	26.8±0.4	–
Ovulation rate	5	0.15±0.02	9	0.21±0.07	5	26.4±1.8	30
Scrotal circumference	6	0.21±0.06	14	0.24±0.04	5	8.7±0.5	12
Disease resistance							
Worm (faecal egg count—FEC)	16	0.27±0.02	–	–	11	30.7±7.2	–
Fleece rot incidence	1	0.17±0.02	–	–	1	149	–
Fleece rot severity	1	0.23±0.02	–	–	1	185	–
Feed intake							
Feed intake	3	0.13±0.03	–	–	3	20.3±1.4	–
Feed intake—adj. wt.	3	0.12±0.05	–	–	3	20.9±1.7	–
Efficiency of wool growth	3	0.25±0.03	–	–	3	29.7±1.2	–

[a] Wool breeds.

[b] Dual-purpose breeds.

were very close to the means reported by Fogarty (1995). The mean heritabilities for ovulation rate (0.15±0.02) and scrotal circumference (0.21±0.06) were higher than the other reproduction traits although they were slightly lower than the means (0.21±0.07 and 0.24±0.04, respectively) reported by Fogarty (1995), which were based on more studies. The reproduction traits generally had very high coefficients of variation, which were similar to Fogarty (1995).

3.1.5. Feed intake and disease resistance

The weighted mean heritability for feed intake was 0.13±0.03 with an average coefficient of variation of 20.3% (Table 2). Among the younger sheep, there was a trend towards increased heritability with age from 9 months (0.08±0.05) to 15 months (0.20±0.08) (Lee et al., 2002), although the pooled estimate for mature ewes (0.12±0.07) was intermediate (Lee et al., 1995). Adjustment for liveweight had little impact on the estimates of heritability.

The weighted mean heritability for worm resistance measured as faecal egg count (Table 2) from 16 independent estimates was moderate (0.27±0.02) with a coefficient of variation of 31±7%. There was one study of fleece rot (Li et al., 1999), which reported heritability estimates of 0.17 for incidence and 0.23 for severity, with very high coefficients of variation (149% and 185%, respectively).

3.2. Maternal heritability and common environmental effects

Maternal heritability for liveweight declined with increasing age from birth to adult (Table 3). For birth weight, the weighted mean maternal heritability was similar to the direct heritability in wool and dual-purpose breeds and somewhat higher in meat breeds in those studies where both components were estimated (Table 3). Maternal heritability for weaning weight was some 56–76% of that for direct heritability and was generally less than 30% of direct heritability for post weaning and adult weights. Comparison of the direct heritability estimates for growth traits shown in Table 1 (all studies) with those in Table 3 (studies that included maternal effects in the model) generally shows a very small reduction in direct heritability estimates when maternal effects are included in the model.

The interpretation of genetic parameter estimates for traits that are influenced by maternal effects in an animal model context is dependent on both the structure and the model used in the analysis. Koots et al. (1994a) reviewed many studies in beef cattle and found no difference between heritability estimates when an animal model or other methods were used or between estimates that did or did not include maternal effects in the animal model. There are several reports in sheep that have shown inflated direct heritability estimates when maternal effects were not included (Maniatis and Pollott, 2002a; Vaez Torshizi et al., 1996; Nasholm and Danell, 1996). However, the very small reduction in direct heritability for growth traits found here when only those studies with maternal effects were included, together with the similarity to Fogarty (1995), which generally did not include maternal effects, indicates little overall impact on the estimates. This might be due to inclusion of the covariance between direct and maternal genetic effects (Hagger and Schneeberger, 1995; Hagger, 2002) or exclusion of sire by environmental effects which inflates the covariance between direct and maternal genetic effects (Maniatis and Pollott, 2002c).

There were significant common environmental effects for growth traits (Table 3), which tended to be higher for birth weight and weaning weight than later weights. Weighted means for the genetic correlations between direct and maternal effects were variable and associated with large standard errors, with half of the estimates not significantly different from zero.

Genetic evaluation of growth traits needs to adopt a model that includes direct and maternal genetic, as well as maternal environmental effects. It is essential to partition maternal environment effects into across year dam effects and litter effects (within year common environmental effect unique to the litter) where multiple births are relatively common. The question of inclusion of genetic covariance for direct and maternal effects in models is an issue which needs to be investigated with appropriate data structure, as well as the nature and impact of sire by year interaction. It has been shown that a negative genetic correlation between direct and maternal genetic effects might be a product of both existing genetic antagonism as well as the sire by year interaction (Hagger, 1998; Maniatis and Pollott, 2002b; Konstantinov and Brien, 2003) and can be influenced by data structure (Maniatis and Pollott, 2003).

For wool traits a significant maternal effect was found in wool breeds for both greasy and clean fleece weight (32% and 21%, respectively, of direct heritability) but not in dual-purpose breeds (Table 3). The permanent environmental effect for fleece weight was highly variable in the wool breeds and only significant

Table 3
Number of literature estimates (n) and weighted mean (±S.E.) of estimates for direct (h^2) and maternal (m^2) heritability, common environmental effects (c^2) and correlation between direct and maternal genetic effects (r_{am}) for growth, wool and reproduction traits

Trait	n[a]	h^2±S.E.[a]	n	m^2±S.E.	n	c^2±S.E.	n	r_{am}±S.E.
Growth								
Birth weight[b]	6	0.21±0.04	6	0.21±0.03	5	0.10±0.02	4	−0.31±0.06
Birth weight[c]	21	0.19±0.02	21	0.18±0.02	21	0.09±0.02	16	−0.08±0.06
Birth weight[d]	6	0.15±0.05	6	0.24±0.03	5	0.19±0.05	5	−0.25±0.13
Weaning weight[b]	9	0.21±0.02	9	0.16±0.04	7	0.06±0.01	6	0.35±0.11
Weaning weight[c]	35	0.16±0.01	35	0.10±0.01	30	0.07±0.01	26	0.34±0.04
Weaning weight[d]	7	0.18±0.04	7	0.10±0.01	7	0.14±0.02	6	0.37±0.05
Post-weaning weight[b]	8	0.30±0.03	8	0.10±0.02	4	0.03±0.03	4	0.18±0.24
Post-weaning weight[c]	15	0.28±0.03	15	0.04±0.01	12	0.05±0.02	10	−0.07±0.13
Post-weaning weight[d]	4	0.22±0.02	4	0.08±0.03	3	0.06±0.01	3	−0.25±0.04
Adult weight[b]	7	0.42±0.03	7	0.04±0.01	6	0.10±0.04	4	0.74±0.15
Adult weight[c]	4	0.40±0.06	4	0.06±0.03	5	0.09±0.04	2	−0.16±0.29
Adult weight[d]	4	0.29±0.02	–	–	–	–	–	–
Daily gain	16	0.15±0.01	16	0.05±0.01	14	0.05±0.01	14	−0.02±0.08
Wool								
Greasy fleece weight[b]	5	0.25±0.06	5	0.08±0.01	4	0.15±0.09	–	–
Greasy fleece weight[c]	8	0.31±0.04	8	0.02±0.01	6	0.11±0.02	–	–
Clean fleece weight[b]	8	0.28±0.01	8	0.06±0.01	4	0.21±0.11	–	–
Reproduction								
Lambs weaned/ewe joined	11	0.07±0.01	–	–	5	0.07±0.02	–	–
Lambs born/ewe joined	19	0.10±0.01	–	–	15	0.04±0.01	–	–
Weight weaned/ewe joined	7	0.13±0.03	–	–	3	0.08±0.02	–	–
Lambs weaned/ewe lambing	8	0.05±0.01	–	–	5	0.04±0.01	–	–
Lambs born/ewe lambing	49	0.13±0.01	–	–	36	0.05±0.01	–	–
Lambs born alive/ewe lambing	2	0.10±0.05	–	–	2	0.05±0.02	–	–
Weight weaned/ewe lambing	11	0.11±0.02	–	–	10	0.03±0.01	–	–
Ewes lambing/ewe joined	18	0.08±0.01	–	–	12	0.04±0.01	–	–
Ewe rearing ability	7	0.06±0.02	–	–	5	0.07±0.02	–	–
Lamb survival	16	0.03±0.01	8	0.05±0.01	–	–	–	–
Embryo survival	4	0.01±0.01	–	–	4	0.07±0.02	–	–
Ovulation rate	5	0.15±0.02	–	–	5	0.11±0.03	–	–
Scrotal circumference	6	0.21±0.06	–	–	–	–	–	–

[a] Only estimates that included maternal heritability (m^2) in the model for growth and wool traits.
[b] Wool breeds.
[c] Dual-purpose breeds.
[d] Meat breeds.

in dual-purpose breeds. For genetic evaluation of fleece weight, a model with direct animal and maternal-genetic effects as well as an animal permanent environmental effect needs to be evaluated.

Very few studies included or reported significant maternal effects in the models for analysis of reproduction traits. The exception was lamb survival (Table 3) in which the maternal heritability was generally as large or larger than the direct heritability (Hall et al., 1995; Lopez-Villalobos and Garrick, 1999; Matos et al., 2000; Morris et al., 2000; Southey et al., 2001). Generally, the permanent environmental effects for reproduction traits were lower than direct heritability with the exception of embryo survival and ewe rearing ability. The preferred model for the analysis of reproduction traits included both direct genetic and permanent environmental effects. Multivariate analysis is preferred to the repeatability model due to an increase in variance components (genetic and environmental) from first to third litters (de Vries et al., 1998; Hagger, 2002; Nagy et al., 1999; Okut et al., 1999).

3.3. Genetic and phenotypic correlations

3.3.1. Wool traits

The weighted mean genetic and phenotypic correlations among wool traits are presented in Table 4. The correlations between greasy and clean fleece weight were very high, with the genetic being 0.86 and phenotypic 0.90. The genetic and phenotypic correlations for fibre diameter and greasy fleece weight (0.36 and 0.31, respectively) and clean fleece weight (0.28 and 0.25, respectively) were moderate and positive. These mean estimates of the correlations were generally similar to those reviewed by Fogarty (1995), although the mean genetic correlations between fibre diameter and fleece weights were slightly lower in his review (0.17 greasy and 0.21 clean fleece weight).

The genetic and phenotypic correlations between fleece weight and the other wool traits were generally low to moderate and similar for greasy and clean fleece weight. The exceptions were for yield where the correlations for clean fleece weight were considerably higher than those for greasy fleece weight (0.38 vs. −0.14 genetic and 0.37 vs. −0.04 phenotypic) and the coefficient of variation of fibre diameter where clean fleece weight had a higher genetic correlation (0.19 vs. 0.09) and lower phenotypic correlation (−0.04 vs. 0.36) than greasy fleece weight. The two measures of variation in fibre diameter (coefficient of variation and standard deviation of fibre diameter) were highly correlated (0.76 genetic and 0.82 phenotypic), although their correlations with fibre diameter differed considerably (−0.10 vs. 0.43 genetic and −0.09 vs. 0.40 phenotypic, respectively). The mean correlations between fibre diameter and standard deviation of fibre diameter involved only two studies (Swan et al., 1995; Hill, 2001), which also reported moderate negative correlations with coefficient of variation of fibre diameter. There were moderately positive genetic correlations between yield and staple length (0.25) and staple strength (0.35), although there was little genetic relationship between staple length and strength (0.05). The confidence intervals were generally small around the weighted mean genetic correlations between fleece weights and fibre diameter, although they were larger for the genetic correlations among other traits. Most of the studies were for the Merino breed, which may be expected to reduce variation among the correlation estimates.

3.3.2. Growth traits

The weighted mean genetic and phenotypic correlations between the various growth traits are shown in Table 5. The genetic correlations were higher for

Table 4
Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations among wool traits with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	GFW	CFW	FD	CVFD	SDFD	SL	SS	YLD
Greasy fleece weight (GFW)		0.90 (12) [0.83 0.94]	0.31 (15) [0.14 0.45]	0.36 (5) [0.18 0.52]	0.15 (2) [−0.17 0.44]	0.32 (5) [0.18 0.45]	0.19 (3) [0.02 0.34]	−0.04 (11) [−0.22 0.14]
Clean fleece weight (CFW)	0.86 (13) [0.70 0.94]		0.25 (21) [0.05 0.43]	−0.04 (8) [−0.19 0.11]	0.10 (2) [−0.21 0.39]	0.33 (7) [0.20 0.45]	0.18 (6) [0.02 0.33]	0.37 (13) [0.16 0.55]
Fibre diameter (FD)	0.36 (18) [0.07 0.59]	0.28 (22) [0.06 0.48]		−0.09 (10) [−0.28 0.10]	0.40 (2) [0.16 0.60]	0.19 (9) [0.01 0.37]	0.23 (6) [0.02 0.42]	0.01 (13) [−0.15 0.18]
Coefficient of variation of FD (CVFD)	0.09 (6) [−0.20 0.37]	0.19 (9) [0.02 0.35]	−0.10 (11) [−0.32 0.14]		0.82 (2) [0.73 0.88]	−0.12 (7) [−0.16 −0.08]	−0.38 (5) [−0.45 −0.31]	−0.13 (4) [−0.24 −0.01]
Standard deviation of FD (SDFD)	0.25 (2) [0.19 0.31]	0.22 (2) [0.17 0.26]	0.43 (2) [0.40 0.46]	0.76 (2) [0.75 0.78]		–	–	−0.13 (2) [−0.22 −0.03]
Staple length (SL)	0.44 (11) [0.00 0.74]	0.36 (7) [0.06 0.61]	0.19 (10) [−0.11 0.45]	−0.06 (7) [−0.27 0.15]	–		0.07 (5) [−0.29 0.41]	0.19 (5) [0.08 0.30]
Staple strength (SS)	0.16 (3) [−0.55 0.74]	0.20 (6) [−0.42 0.70]	0.37 (6) [−0.03 0.71]	−0.52 (5) [−0.71 −0.26]	–	0.05 (5) [−0.60 0.66]		0.15 (4) [0.08 0.22]
Yield (YLD)	−0.14 (12) [−0.36 0.09]	0.38 (14) [0.20 0.54]	0.04 (14) [−0.17 0.24]	−0.08 (5) [−0.38 0.24]	−0.10 (2) [−0.37 0.18]	0.25 (5) [0.11 0.38]	0.35 (4) [0.09 0.57]	

Table 5
Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations among growth traits with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	BW	WW	PWW	AW	G/D
Birth weight (BW)		0.37 (10) [0.22 0.51]	0.32 (7) [0.19 0.44]	0.26 (5) [0.20 0.33]	0.13 (1)
Weaning weight (WW)	0.47 (14) [−0.17 0.83]		0.70 (9) [0.49 0.84]	0.56 (12) [0.38 0.70]	0.16 (1)
Post-weaning weight (PWW)	0.29 (8) [−0.27 0.71]	0.85 (11) [0.32 0.97]		0.74 (9) [0.51 0.87]	–
Adult weight (AW)	0.22 (7) [−0.26 0.61]	0.75 (16) [0.13 0.95]	0.93 (11) [0.65 0.99]		0.34 (1)
Growth rate (G/D)	0.27 (6) [−0.23 0.65]	0.79 (4) [−0.78 1.00]	0.19 (1)	0.78 (1)	

weights at adjacent age classes and increased with age from birth to adult. The phenotypic correlations were generally slightly lower than the corresponding genetic correlations. The genetic correlations among weaning, post-weaning and adult weights were very high and ranged from 0.75 to 0.93. Birth weight had a moderate genetic correlation with weaning weight (0.47) and lower correlations with post weaning (0.29) and adult (0.22) weights. Growth rate was moderately genetically correlated with birth weight (0.27) and highly correlated with weaning weight (0.79). These weighted mean genetic and phenotypic correlations were remarkably similar to those reported by Fogarty (1995). However, the wide confidence intervals generally found for the genetic correlations reflects the variation between different studies. There is a need for more estimates of these genetic correlations from larger data sets and for the inclusion of maternal components in the models.

3.3.3. Carcass and meat traits

The weighted mean correlations among carcass traits and between live weight and carcass traits are presented in Table 6. These correlations are from reports that cover a range in ages from 5 to 18 months. There were moderate genetic correlations between live weight and fat depth (0.36) and muscle depth (0.34) and between fat depth and muscle depth (0.33) measured in live animals which were similar to the corresponding phenotypic correlations. The mean genetic correlations between live measurements of eye muscle depth, width and area were very high (0.78–0.99), with the corresponding phenotypic correlations being slightly lower (0.56–0.90). The mean genetic correlations between liveweight and muscle dimensions in the carcass were moderate (0.24–0.28) and similar to the phenotypic correlations. The mean genetic correlations between carcass weight and carcass fat depth (0.39) and muscle depth (0.54) were higher than the correlations between liveweight and corresponding measurements in live animals using ultrasound. Carcass fat depth had negative mean genetic correlations with muscle dimensions (−0.3), with the phenotypic correlations being smaller in magnitude (−0.05 to −0.18). The mean genetic correlation between eye muscle depth and width was only moderate (0.28), although the correlations between eye muscle area and depth (0.86) or width (0.74) were much higher. Fogarty (1995) reported correlations between ultrasonic fat measurement and weight in live sheep ranging from 0.31 to 0.46 (genetic) and 0.25 to 0.51 (phenotypic) at various ages which are consistent with the corresponding mean correlations found in this study. Adjustment of fat depth in live animals for liveweight reduced both the genetic and phenotypic correlations to near zero which was expected and was similar to Fogarty (1995).

The weighted mean genetic correlation for dressing yield and carcass conformation (0.45) was higher than the correlations for dressing yield with eye muscle area (0.35) and fat depth at the C site (0.25), with that at the GR site being negative (−0.21) from one report (Table 7). The genetic correlation between fat depth at the C site and conformation was low (0.13). The mean phenotypic correlations were generally similar or lower than the corresponding genetic correlations. Different measures of carcass fatness (GR and C sites) were highly correlated both at the genetic (0.93) and phenotypic (0.56) level. The mean genetic correlation between fat depth (C site) and eye muscle area was slightly negative (−0.09). Information on the relationship between carcass and meat quality indicator traits (meat pH and colour) is scant and estimates were only available from one study of limited size (Table 7).

Table 6

Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations among carcass traits and weight with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	LW	FATl	FATla	EMDl	EMWl	EMAl	CW	FATc	EMDc	EMWc	EMAc
Live weight (LW)		0.36 (9) [0.16 0.53]	0.02 (10) [−0.11 0.16]	0.33 (6) [−0.18 0.69]	–	–	–	−0.06 (1)	0.32 (8) [−0.20 0.70]	0.25 (2) [−0.44 0.75]	0.28 (2) [−0.48 0.80]
Fat depth—live (FATl)	0.36 (9) [−0.44 0.84]		–	0.30 (10) [−0.02 0.56]	0.34 (4) [0.00 0.61]	0.51 (3) [0.24 0.70]	–	0.51 (1)	–	–	–
Fat depth—live, adj. wt. (FATla)	0.03 (10) [−0.39 0.44]	–		–	–	–	–	–	–	–	–
Eye muscle depth—live (EMDl)	0.34 (6) [−0.23 0.73]	0.33 (10) [−0.28 0.76]	–		0.56 (4) [0.47 0.64]	0.90 (3) [0.86 0.92]	–	–	–	–	–
Eye muscle width—live (EMWl)	–	0.10 (4) [−0.33 0.50]	–	0.78 (4) [−0.28 0.98]		0.87 (3) [0.83 0.89]	–	–	–	–	–
Eye muscle area—live (EMAl)	–	0.40 (3) [0.06 0.67]	–	0.99 (3) [0.97 1.00]	0.95 (3) [0.93 0.97]		–	–	–	–	–
Carcass weight (CW)	–	–	–	–	–	–		0.54 (2) [0.48 0.59]	0.54 (2) [0.36 0.67]	0.42 (2) [0.21 0.60]	0.57 (1)
Fat depth—carcass (FATc)	−0.12 (1)	0.77 (1)	–	–	–	–	0.39 (2) [0.32 0.46]		−0.05 (2) [−0.17 0.08]	−0.18 (2) [−0.37 0.02]	−0.02 (3) [−0.09 0.06]
Eye muscle depth—carcass (EMDc)	0.28 (8) [−0.25 0.68]	–	–	–	–	–	0.54 (2) [0.35 0.69]	−0.33 (2) [−0.58 −0.02]		0.23 (3) [−0.19 0.58]	0.74 (2) [0.12 0.95]
Eye muscle width—carcass (EMWc)	0.24 (2) [−0.17 0.59]	–	–	–	–	–	0.32 (2) [−0.07 0.62]	−0.30 (2) [−0.54 −0.01]	0.28 (3) [−0.27 0.69]		0.62 (2) [0.39 0.79]
Eye muscle area—carcass (EMAc)	0.27 (2) [−0.33 0.71]	–	–	–	–	–	0.59 (1)	−0.09 (3) [−0.34 0.17]	0.86 (2) [0.77 0.91]	0.74 (2) [0.62 0.82]	

LW includes post-weaning and adult weight.

Table 7
Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations among carcass and meat traits with number of estimates in parenthesis ( ) and 95% confidence interval in brackets [ ]

Trait	CONF	DY	FATC	FATGR	EMA	pH	L^*
Conformation (CONF)		0.26 (2) [0.12 0.38]	0.15 (3) [0.05 0.25]	–	0.26 (2) [0.23 0.29]	–	–
Dressing yield (DY)	0.45 (2) [0.25 0.61]		0.25 (3) [0.08 0.40]	0.06 (1)	0.27 (3) [−0.27 0.63]	0.06 (1)	−0.03 (1)
Fat C site (FATC)	0.13 (3) [0.03 0.22]	0.14 (3) [−0.06 0.33]		0.56 (2) [−0.05 0.86]	−0.02 (3) [−0.09 0.06]	−0.03 (1)	0.06 (1)
Fat GR site (FATGR)	–	−0.21 (1)	0.93 (2) [−0.14 1.00]		0.01 (1)	−0.11 (1)	0.06 (1)
Eye muscle area (EMA)	0.27 (2) [0.11 0.41]	0.35 (3) [−0.37 0.81]	−0.09 (3) [−0.34 0.17]	−0.00 (1)		0.02 (1)	−0.12 (1)
Meat pH	–	0.19 (1)	0.16 (1)	0.14 (1)	−0.02 (1)		−0.32 (1)
Meat colour L^*	–	−0.24 (1)	−0.34 (1)	−0.11 (1)	−0.12 (1)	−0.56 (1)	

There were generally very wide confidence intervals for the correlations among carcass and meat traits. This is a reflection of the considerable variation between estimates from the few studies, which generally had small data sets. The differences between the studies due to breed (wool and meat) and age of animals may have also contributed to the variation between studies.

3.3.4. Reproduction traits

There was a very high weighted mean genetic correlation (0.84) between the number of lambs weaned and the number of lambs born on a per ewe joined basis (Table 8). The genetic correlations for weight of lamb weaned (per ewe joined) with number of lambs weaned (0.80) was higher than with the number of lambs born (0.60), suggesting that the

Table 8
Weighted means of literature estimates for genetic (below diagonal) and phenotypic (above diagonal) correlations among reproduction traits with number of estimates in parenthesis ( ) and 95% confidence interval in brackets [ ]

Trait	NLW/EJ	NLB/EJ	WW/EJ	NLW/EL	NLB/EL	WW/EL	EL/EJ	NLW/NLB
Number of lambs weaned/ewe joined (NLW/EJ)		0.73 (4) [0.48 0.87]	0.93 (3) [0.91 0.95]	–	0.46 (3) [0.05 0.73]	–	0.54 (3) [0.34 0.76]	0.76 (3) [0.18 0.95]
Number of lambs born/ewe joined (NLB/EJ)	0.84 (6) [−0.43 0.99]		0.59 (3) [0.30 0.77]	–	0.80 (4) [0.52 0.92]	0.78 (3) [0.76 0.79]	0.72 (4) [0.51 0.85]	−0.09 (3) [−0.35 0.18]
Weight weaned/ewe joined (WW/EJ)	0.80 (4) [−0.34 0.99]	0.60 (4) [0.00 0.89]		–	0.13 (1)	–	0.68 (1)	0.64 (1)
Number of lambs weaned/ewe lambing (NLW/EL)	−0.04 (1)	0.00 (1)	0.10 (1)		0.23 (5) [−0.67 0.85]	–	–	–
Number of lambs born/ewe lambing (NLB/EL)	0.62 (4) [−0.52 0.97]	0.89 (5) [0.62 0.97]	0.05 (2) [−0.15 0.25]	0.70 (7) [−0.48 0.98]		0.23 (5) [−0.67 0.85]	0.03 (5) [−0.03 0.09]	−0.13 (4) [−0.37 0.14]
Weight weaned/ewe lambing (WW/EL)	0.16 (1)	0.84 (4) [−0.66 1.00]	0.09 (1)	0.89 (6) [−0.19 1.00]	0.57 (11) [−0.48 0.98]		–	–
Fertility (EL/EJ)	0.73 (4) [−0.18 0.97]	0.79 (5) [−0.08 0.98]	0.70 (2) [−0.80 0.99]	0.42 (1)	0.44 (7) [−0.12 0.79]	0.32 (1)		0.04 (4) [−0.03 0.12]
Ewe rearing ability (NLW/NLB)	0.63 (4) [−0.60 0.97]	0.52 (4) [−0.99 1.00]	0.41 (2) [−0.61 0.92]	0.55 (2) [−0.19 0.89]	−0.14 (6) [−0.94 0.90]	0.14 (1)	0.44 (5) [−0.94 0.99]	

number of lambs weaned and weight weaned are genetically similar traits. The phenotypic correlations between these traits were also very high (0.59–0.93).

The number of lambs born per ewe joined was highly correlated with both its components, lambs born per ewe lambing or litter size (genetic 0.89, phenotypic 0.80) and fertility (genetic 0.79, phenotypic 0.72). These correlations were higher than those for number of lambs weaned per ewe joined with litter size (genetic 0.62, phenotypic 0.46) and fertility (genetic 0.73, phenotypic 0.54). There were moderately high correlations between the number of lambs weaned per ewe joined and its other component ewe rearing ability (genetic 0.63, phenotypic 0.76). Ewe fertility was moderately genetically correlated with both ewe rearing ability (0.44) and litter size (0.44), although the phenotypic correlations were close to zero. On the other hand litter size had a small negative genetic correlation with ewe rearing ability (−0.14). There was also one report relating fertility in ewes and scrotal circumference in rams with a genetic correlation of 0.20 (Fossceco and Notter, 1995).

The genetic correlations between reproduction traits were generally highly variable despite the traits having low heritability and they were generally higher than the phenotypic correlations which were more uniform. This may be due to breed differences, modelling and data structure used to estimate the parameters. Accurate estimation of genetic correlations requires very large numbers of individuals of known relationship with data on both traits. These weighted mean genetic and phenotypic correlations among reproduction traits were similar to those reported by Fogarty (1995).

3.3.5. Growth with wool traits

The genetic and phenotypic correlations between live weight at various ages and the wool traits, greasy and clean fleece weight and fibre diameter, were generally positive and moderate in magnitude (Table 9). The correlations generally increased with age from birth to post weaning weight but declined slightly to adult weight which included reports using mature weights. In contrast the relationship between live weight and coefficient of variation of fibre diameter and yield were generally negative and small. Correlations between staple length and strength with live weight were generally positive and weak. The only exception was the genetic correlation between adult weight and staple strength (−0.11).

3.3.6. Growth with reproduction traits and worm resistance

The weighted mean genetic correlations between the reproduction traits and live weight at various ages are shown in Table 10. The genetic correlations for

Table 9
Weighted means of literature estimates for genetic and phenotypic correlations between live weights at birth (BW), weaning (WW), post-weaning (PWW) and adult (AW) and wool traits with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	Genetic correlation				Phenotypic correlation			
	BW	WW	PWW	AW	BW	WW	PWW	AW
Greasy fleece weight (GFW)	0.21 (4) [0.16 0.26]	0.24 (12) [−0.04 0.48]	0.35 (8) [−0.09 0.68]	0.22 (12) [−0.21 0.58]	0.24 (3) [0.05 0.41]	0.25 (10) [0.11 0.39]	0.44 (8) [0.25 0.59]	0.37 (11) [0.15 0.56]
Clean fleece weight (CFW)	0.11 (3) [0.00 0.22]	0.21 (7) [−0.06 0.45]	0.24 (10) [−0.14 0.56]	0.21 (11) [−0.14 0.51]	0.24 (3) [0.07 0.41]	0.31 (7) [0.05 0.53]	0.39 (10) [0.14 0.60]	0.35 (11) [0.12 0.55]
Fibre diameter (FD)	0.18 (2) [−0.16 0.48]	0.05 (9) [−0.28 0.36]	0.20 (11) [−0.45 0.71]	0.15 (13) [−0.21 0.47]	−0.05 (2) [−0.11 −0.01]	0.05 (8) [−0.06 0.16]	0.16 (11) [−0.06 0.36]	0.13 (12) [0.00 0.26]
Coefficient of variation of FD (CVFD)	–	0.02 (1)	−0.17 (4) [−0.33 0.00]	−0.08 (6) [−0.43 0.29]	–	0.05 (1)	−0.17 (4) [−0.27 −0.06]	−0.06 (6) [−0.26 0.14]
Staple length (SL)	0.05 (1)	0.17 (7) [−0.11 0.42]	0.16 (3) [−0.13 0.43]	0.01 (4) [−0.57 0.58]	–	0.01 (7) [−0.03 0.05]	0.20 (3) [0.09 0.31]	0.10 (4) [−0.11 0.30]
Staple strength (SS)	–	0.21 (2) [−0.61 0.81]	0.30 (1)	−0.11 (2) [−0.14 −0.08]	–	0.06 (2) [−0.13 0.24]	0.22 (1)	0.04 (2) [0.01 0.07]
Yield (YLD)	−0.25 (2) [−0.27 −0.24]	−0.07 (4) [−0.24 0.10]	−0.14 (5) [−0.32 0.06]	0.00 (7) [−0.39 0.38]	0.05 (2) [0.02 0.08]	0.00 (4) [−0.03 0.03]	−0.03 (5) [−0.10 0.04]	0.02 (7) [−0.01 0.05]

Estimates for growth rate included in WW.

Table 10
Weighted means of literature estimates for genetic and phenotypic correlations between weights at birth (BW), weaning (WW), post-weaning (PWW) and adult (AW) and reproduction traits and worm resistance (FEC) with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	Genetic correlation				Phenotypic correlation			
	BW	WW	PWW	AW	BW	WW	PWW	AW
Number of lambs weaned/ewe joined (NLW/EJ)	0.00 (1)	0.18 (2) [0.00 0.35]	0.29 (1)	0.33 (4) [0.16 0.48]	–	0.03 (1)	0.10 (1)	0.09 (4) [0.05 0.12]
Number of lambs born/ewe joined (NLB/EJ)	0.10 (1)	0.15 (2) [−0.45 0.65]	0.23 (1)	0.15 (10) [−0.38 0.61]	–	0.04 (1)	0.12 (1)	0.03 (10) [−0.06 0.12]
Weight weaned/ewe joined (WW/EJ)	–	0.75 (1)	0.77 (1)	0.70 (6) [0.30 0.89]	–	0.13 (1)	0.24 (1)	0.21 (6) [0.07 0.34]
Number of lambs weaned/ewe lambing (NLW/EL)	−0.09 (4) [−0.38 0.22]	−0.05 (4) [−0.82 0.78]	–	–	–	–	–	–
Number of lambs born/ewe lambing (NLB/EL)	0.12 (7) [−0.28 0.49]	0.29 (11) [−0.33 0.73]	0.17 (7) [0.09 0.24]	0.27 (3) [−0.58 0.84]	0.09 (1)	0.06 (5) [0.00 0.12]	0.01 (6) [−0.03 0.06]	−0.02 (1)
Weight weaned/ewe lambing (WW/EL)	0.12 (4) [−0.27 0.48]	0.10 (1)	0.06 (4) [−0.18 0.29]	0.68 (2) [0.34 0.86]	–	–	–	0.18 (1)
Fertility (EL/EJ)	–	−0.28 (2) [−0.36 0.20]	–	0.40 (2) [−0.43 0.86]	–	0.09 (2) [−0.28 0.44]	–	0.11 (2) [0.02 0.21]
Ewe rearing ability (NLW/NLB)	–	–	–	0.20 (2) [0.09 0.31]	–	–	–	0.03 (2) [−0.03 0.09]
Worm resistance (FEC)	0.11 (1)	−0.03 (5) [−0.34 0.29]	−0.24 (4) [−0.56 0.14]	−0.12 (3) [−0.45 0.23]	0.07 (1)	−0.03 (5) [−0.15 0.09]	−0.08 (4) [−0.18 0.03]	−0.07 (3) [−0.12 0.02]

Estimates for growth rate included in WW.

number of lambs born and weaned (per ewe joined) with weaning, post-weaning and adult weights were positive and moderate in magnitude, while those with birth weight were close to zero. The correlation estimates were highly variable and the means had large confidence intervals. The weight of lamb weaned (per ewe joined) was highly genetically correlated with liveweight (>0.70). For weight of lamb weaned (per ewe lambing), there was a similar genetic correlation with adult weight (0.68), although the correlation estimates with weights at the younger ages were considerably lower. Adult weight was moderately genetically correlated with ewe fertility (0.40) and ewe rearing ability (0.20), although there was a negative correlation between weaning weight and ewe fertility (−0.28). The phenotypic correlations were considerably lower than the genetic correlations. Scrotal circumference had genetic correlation estimates with early liveweight (<4 months) of greater than 0.6 in three reports (see Safari and Fogarty, 2003).

Ap Dewi et al. (2002) reported genetic correlations between reproduction and carcass traits measured in live animals at 14 months of age. These genetic correlations for weight of lamb weaned per ewe lambing and litter size with muscle depth were 0.28 and 0.35, respectively, and for fat depth were 0.20 and −0.01, respectively. The weighted genetic and phenotypic correlations between worm resistance (measured as faecal egg count) and growth traits were generally negative (favourable) with the exception of birth weight where a small positive correlation was observed in one study (Table 10).

3.3.7. Wool with reproduction traits

The weighted mean genetic correlations between fleece weight and the various reproduction traits were small and negative, except for weight of lamb weaned per ewe joined (0.16) and scrotal circumference (0.15) (Table 11). There were few estimates of correlations of reproduction with fibre diameter or staple length and they were generally low. All of the phenotypic

Table 11
Weighted means of literature estimates for genetic and phenotypic correlations between wool fleece weight (FW), fibre diameter (FD) and staple length (SL) and reproduction traits with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	Genetic correlation			Phenotypic correlation	
	FW	FD	SL	FW	FD
Lambs weaned/ewe joined (NLW/EJ)	−0.12 (5) [−0.39 0.16]	0.00 (2) [−0.25 0.25]	−0.20 (1)	0.00 (4) [−0.15 0.15]	0.01 (2) [−0.06 0.09]
Lambs borne/ewe joined (NLB/EJ)	−0.13 (4) [−0.37 0.12]	−0.17 (1)	−0.05 (1)	−0.03 (3) [−0.15 0.15]	−0.03 (1)
Weight weaned/ewe joined (WW/EJ)	0.16 (8) [−0.37 0.60]	0.15 (5) [−0.10 0.39]	–	0.01 (8) [−0.10 0.12]	0.06 (5) [−0.01 0.13]
Lambs weaned/ewe lambing (NLW/EL)	−0.10 (5) [−0.66 0.53]	–	−0.45 (4) [−0.99 0.92]	–	–
Lambs born/ewe lambing (NLB/EL)	−0.05 (8) [−0.45 0.36]	0.30 (1)	0.00 (4) [−0.03 0.03]	−0.01 (3) [−0.05 0.00]	0.07 (1)
Weight weaned/ewe lambing (WW/EL)	−0.07 (4) [−0.58 0.48]	–	−0.01 (4) [−0.16 0.15]	–	–
Scrotal circumference	0.15 (1)	0.22 (1)	–	0.08 (1)	−0.05 (1)

correlations were close to zero, with none reported for staple length.

3.3.8. Wool with meat, carcass, worm resistance and feed intake traits

The weighted mean genetic correlations for wool weight (clean and greasy) with fat depth (−0.19) and muscle depth (0.23) measured in both live animals and carcasses were moderate and varied in sign, while those for fibre diameter were 0.18 and 0.07 respectively (Table 12). The two studies with wool and meat quality traits (pH and colour) reported estimates of genetic correlations that varied considerably (Safari and Fogarty, 2003).

Worm resistance had very low genetic correlations with wool traits. Feed intake was positively genetically correlated with wool weight (0.14), although the correlation was reduced to near zero when feed intake was adjusted for live weight. There was a higher genetic correlation between fibre diameter and feed intake (0.39 and 0.25 when adjusted for weight), although the phenotypic correlations were low.

4. Summary of parameter estimates

Fig. 1 presents a summary of the numbers of available estimates of genetic parameters from the literature over the last decade for a wide range of sheep production traits. The number of parameter estimates from independent data sets used to obtain the weighted means in the earlier tables for herit-

Table 12
Weighted means of literature estimates for genetic and phenotypic correlations between wool fleece weight (FW) and fibre diameter (FD) and carcass/meat, worm resistance and feed intake traits with the number of estimates in parenthesis ( ) and the 95% confidence interval in brackets [ ]

Trait	Genetic correlation		Phenotypic correlation	
	FW	FD	FW	FD
Fat depth	−0.19 (5) [−0.50 0.17]	0.18 (4) [−0.39 0.65]	0.17 (3) [−0.03 0.36]	0.04 (3) [−0.02 0.10]
Eye muscle depth	0.23 (2) [−0.13 0.53]	0.07 (2) [0.00 0.14]	0.02 (1)	0.06 (1)
Meat pH	0.05 (2) [−0.54 0.70]	−0.40 (2) [−0.97 0.86]	0.03 (1)	0.01 (1)
Meat colour *L**	0.13 (2) [−0.54 0.70]	−0.08 (2) [−0.97 0.97]	−0.01 (1)	−0.06 (1)
Worm resistance (FEC)	0.00 (4) [−0.17 0.18]	0.01 (3) [−0.28 0.30]	0.00 (4) [−0.03 0.03]	−0.02 (3) [−0.10 0.05]
Feed intake (FI)	0.14 (2) [−0.16 0.41]	0.39 (2) [0.23 0.54]	0.13 (2) [0.05 0.21]	0.07 (2) [0.04 0.10]
Feed intake—adj. wt.	0.01 (2) [−0.05 0.07]	0.25 (2) [−0.21 0.62]	−0.07 (2) [−0.23 0.08]	0.01 (2) [−0.02 0.04]

	Wool						Growth				Carcass and meat										Reproduction							
	CFW	FD	YLD	CVFD	SL	SS	BW	WW	PW	AW	FATI	EMDI	CW	FATG	FATC	EMDc	DY	LMY	pH	L*	NLW	NLB	WW	EL	LB/EL	LW/LB	FEC	FI
CFW	****																											
FD	****	****																										
YLD	***	***	***																									
CVFD	**	***	*	***																								
SL	**	**	*	**	****																							
SS	**	**	*	*	*	***																						
BW	*	*	*		+		****																					
WW	**	**	*	+	**	*	***	****																				
PWW	**	***	*	*	*	+	**	***	****																			
AW	***	***	**	**	*	*	**	***	***	****																		
FATI	*	*					+	*	**	***	****																	
EMDI							+	*	*	*	**	***																
CW											+		*															
FATGR	*	*	+			+				+	+			*														
FATC	+	+	+			+				+	+		*	*	**													
EMDc	*	*	+			+			+	+			*	*	*	*												
DY										+				+	*	*	*											
LMY													+			+		*										
pH	*	*	+			+				+				+	+	+	+		*									
L*	*	*	+			+				+				+	+	+	+		+	*								
NLW/EJ	*	*			*^{B}		*^{B}	*	+	*											***							
NLB/EJ	*	+			+		+	*	+	**											**	***						
WW/EJ	**	*	+		*^{B}		*^{B}	+	*^{B}	**	+^{B}	+^{B}									*	*	**					
EL/EJ	+							*		*											*	*	*	***				
NLB/EL	**	+			*		**	**	**	**											*	*	*	**	****			
NLW/LB	*									*											*	*	**	**	**	**		
FEC	*	*		*	+	*	+	*	*	*																	***	
FI	*	*		*						*	*																	*

Fig. 1. Summary of the numbers of estimates^{A} for heritability (on diagonal) and genetic correlations (below diagonal) for sheep production traits. See text and Table 1–12 for definition of traits. ^{A}+=1; *=2–5; **=5–10; ***=11–20; ****= >20 estimates. ^{B}Correlations based on per ewe lambing.

abilities and genetic correlations are categorised to show where deficiencies exist. The weighted mean heritability estimates for the major wool traits (clean fleece weight, fibre diameter and staple length) and all the growth traits were based on more than 20 independent estimates, with the other wool traits based on more than 10 independent estimates. The mean heritability estimates for the carcass and meat traits are based on very few estimates except for fat (27) and muscle depth (11) in live animals. There were more than 10 independent estimates of heritability for the reproduction traits, except for weight of lamb weaned and the component trait ewe rearing ability. There were more than 10 independent estimates of heritability for worm resistance measured as faecal egg count (FEC), but few estimates for other sheep disease traits or feed intake.

The mean genetic and phenotypic correlations, in contrast to heritability, were based on considerably smaller numbers of independent estimates. There were a moderate number (>10) of estimates of genetic correlations among most of the wool and growth traits, although there were fewer estimates for the wool quality traits and for birth weight with the other growth traits. There were also only small numbers of estimates of correlations among the reproduction traits with very few among the carcass and meat traits.

Estimates of genetic correlations between the groups of different production traits were very sparse. There were a moderate number of estimates of genetic correlations between live weight and wool traits and between later live weights and fat depth in live animals. However, there were almost no estimates of genetic correlations between carcass/meat traits and reproduction, worm resistance or feed intake. Further, there were no genetic correlations between reproduction traits and worm resistance or feed intake.

The standard errors of the weighted mean heritabilities were equivalent to or smaller than the corresponding values in Fogarty (1995), even though a more conservative approach was adopted here using a mixed model to incorporate the within study variance component. In beef cattle, Koots et al. (1994a) showed that systematic effects, such as breed, country, management, etc., only accounted for a small proportion of the observed variance in heritability estimates from different studies. We found that, for the major wool traits (fleece weight, fibre diameter and yield) and most growth traits in wool and dual-purpose breeds, there was very little or no contribution to the variance of the weighted means for heritability from the between study component. This indicates that the reasonably large numbers of reports for each of these traits were consistent and the same parameters for heritability could be used in different sheep populations. For most of the reproduction and wool quality traits and the growth traits in meat breeds, there was a sizeable contribution to the variance from the between study component. It was generally much smaller (10 to 200 fold) than the within study component, except for the growth traits in meat breeds in which it was equal to or larger than the within study component of variance. This indicates that more precise estimates of heritability may be required from large data sets representing varying sheep populations as there may be real differences in parameters for these traits in different sheep populations.

The weighted mean genetic correlations for most of the traits were associated with wide confidence intervals that reflected the generally large variation between reports and the relatively small data sets (number of sires) that resulted in large standard errors for the individual estimates. Weighted mean phenotypic correlations showed much narrower confidence intervals, even though they were based on smaller numbers of estimates than the genetic correlations.

Breeding objectives for sheep production are becoming more complex. In recent years, in Australia at least, there has been a trend towards increasing economic value for meat production relative to wool and a greater need for products, both wool and meat, to meet particular quality and other specifications as well as the demand for flocks that have reduced costs of management. This has led many sheep breeders to combine wool and meat as well as quality and other traits such as disease resistance into their breeding objectives. Hence, there is an urgent need to provide accurate estimates of genetic parameters and in particular correlations between the groups of production traits with high economic value such as reproduction, carcass and meat, disease resistance and feed intake, as well as wool and growth traits. These parameters are required for accurate genetic evaluation of animals and the development of optimum breeding objectives and selection indexes that will have outcomes that can be predicted with confidence.

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