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Heritability estimates and genotype by environment interactions for worm egg count (WEC) in Australian sheep

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Introduction

Worm egg count (WEC) can be used for selecting worm resistant sheep. More and more records are now present in the Sheep Genetics (SG) database. The Sheep CRC collected WEC at various ages from all information nucleus flocks (INF). The sheep CRC dataset is based on a design where many common sires are used across a range of research flocks across Australia, hence it could be a valuable experimental design for estimating interactions between sire breeding values and environment. Furthermore, the CRC data were based on natural challenge with WEC samples taken only when sufficient levels of WEC were identified on a flock basis. As a result, the time of the year and the age of the animals at WEC measurement varied between breeds and sites. The aims of this report were to use the CRC data to;
1) estimate heritability of WEC by sire breed types, age of animal at observation (Ageatobs) and flocks (sites)
2) evaluate the significance of GxE for WEC across age stages and flocks by multi-trait methods (MT)
3) investigate the sires by Ageatobs interactions by random regression methods (RR)

Materials and methods

There are 3 important worm species identified for worm egg count (WEC) in the CRC database. Only WEC from *Trichostrongylus spp.* was extracted for the study to avoid the confounding of worm specie difference with the other factors such as breeds, flocks and age stages. The total of 23,070 records from 18,781 animals with 505 sires and 8,644 dams on WEC data was extracted from the CRC database containing 9 INF sites from 2007 to 2011, among which were 14,529 animals with one observation, 4,215 animals with two observations and 37 animals with three observations. The raw WEC values were cube root transformed before genetic analyses. Variance and covariance components were estimated using ASREML. Two additive genetic relationship matrices were calculated based on the pedigree file contained 34,080 animals with 3,086 sires and 12,647 dams and with the option to include 87 genetic groups for the base animals fitted as a fixed effects or leaving those base animals as unknown parents.

Univariate analyses

Statistical model:
$$\text{WEC} = \mu + \text{CG} + \text{BT} + \text{Sire breed} + \text{Dam breed} + \text{Sire breed type . dam breed type} +$$
$$\text{Ageatobs} + \text{Age of dam} + \text{Age of dam2} + \text{animal} + (\text{SBF}) + \text{error}$$
where contemporary groups (CG) formed using INF flock, year, sex, breed type and date of measurement were fitted as fixed effects (total of 209 levels across the full data set). Additional fixed effects included birth type (BT, 1 to 5), Sire Breed (19 levels), Dam Breed (7 levels), Sire breed type by dam breed type interaction (15 levels), Ageatobs (covariate) as well as age of dam and its quadratic polynomial. Sire by flock interaction (SBF) was the optional term fitting as random effect in the

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models to compare its importance and the influence of this term on the heritability estimates. There were total of 64 univariate analyses which were combinations of four scenarios;

1) Four data sets: the full data set with all sire breed types, and subsets of each sire breed type (Merino, Maternal and Terminal)
2) Four age-stages: weaning (W, 63-117 day), post-weaning (P, 83-224 day), yearling (Y, 333-434 day) and hogget (H, 455-686 day)
3) With sire by flock (SBF) or without SBF in the models; 4) With genetic groups (n=87) in the pedigree for base animals or not.

Preliminary results demonstrated that significant SBF effect were present in these data. In order to test the effect of SBF was not caused by random chance, a permutation test was conducted by randomly swapping flocks around over sires to make a new SBF code for each animal with WEC observation, then estimating variance for new SBF code. This process was repeated 50 times.

GxE analyses

There are usually three methods to investigate GxE in animal breeding. Firstly, fitting GxE interaction term in the model is the traditional step to check significance level of the interaction term. Secondly, estimating genetic correlations using multiple trait models which assumes performance in each particular environment is a separate trait is the commonly used method to quantify the extent of GxE. Both methods assume that environment can be classified into discrete groups. Thirdly, when the environment can be described as a continuous gradient, random regression model (RR) is a viable alternative to quantify the extent of GxE. In this study, two types of GxE were investigated, i.e. by age of animal (or age stage) and by INF sites.

GxE for four age-stages

The MT and RR methods were used to investigate the extent of GxE for WEC observed at differ age of animal. As most of the WEC observations were from 4 age stages, i.e. weaning (W), post weaning (P), yearling (Y) and hogget (H), WEC observed from these 4 age stages were assumed to be separate traits for each age stage, a single analysis by fitting all four traits in the models were conducted to estimate heritabilities and genetic correlations among age stages. Estimates from two models (with SBF vs. without SBF) were compared.

For the RR method, the total of 22,849 records from age of 61 to 560 days combining all sire breed types were analysed simultaneously by fitting Ageatobs as covariate to study the trend of genetic parameters along the age of animal for WEC, which the statistical model is as below**:**

$$WEC = \mu + CG + BT + \text{Sire breed} + \text{Dam breed} + \text{Sire breed type} . \text{Dam breed type} +$$
$$\text{Ageatobs} + \text{Age of dam} + \text{Age of dam2} + (SBF) + \sum_{m=0}^{n-1} c_m z_m + error$$

where different orders (n=1 to 5) of Legendre polynomials were fitted for each sire, c_m was regression coefficients for sire, z_m is the standardized covariates for the Ageatobs. Homogeneous error variance and heterogeneous error variances with 4 groups of age (<100 day, between 100 and 224 day, between 293 and 343 day, and > 455 day) approximately corresponding to the 4 age stages were compared. Two models with sire by flock and without sire by flock were also compared. All the other notations were the same as outlined above. Sire variance-covariance matrix for ages was calculated as $G = z'Cz$ were C is the estimated variance-covariance matrix of the polynomial coefficients, z is a matrix containing the standardized covariates for the Ageatobs. Additive variance-covariance was equal to 4 times the sire variance-covariance.

GxE between INF sites

The two methods of fitting a random interaction term and MT model were used to study GxE between flocks. The sire by flock (SBF) interactions was fitted as a random effect in the univariate analyses.

The MT method assumed WEC observed from the 8 INF sites were separate traits. A complete set of bivariate analyses among 8 traits were performed for each trait combinations to estimated genetic correlation matrix. The data used in these analyses were only from W and P stages to reduce the confounding of GxE between age stages and INF sites.

For all genetic correlations between age stages and flocks, the corresponding numbers of animals or sires with both observations were summarized.

Table 1. Number of observations across flocks and age-stages by sire breed types

Sire breed type		M	W	P	PW	Y	H	A	Total
Merino	IN01		296	1076		723	227		2322
	IN02			507	72	146	173	26	924
	IN03	114	14	393			204		725
	IN04		397	267		93	175		932
	IN05		1	328			185	1	515
	IN06	2	318	336					656
	IN07			1100		280	286	38	1704
	IN08		405	1041			441		1887
	subtotal	116	1431	5048	72	1242	1691	65	9665
Maternal	IN01		114	564		216	139		1033
	IN02			389	1	30	188		608
	IN03	153	28	300			282		763
	IN04		309	171		110	120		710
	IN05		2	431			236		669
	IN06		219	246					465
	IN07			389		49	77		515
	IN08		391	601			184		1176
	IN09			22					22
	subtotal	153	1063	3113	1	405	1226		5961
Terminal	IN01		252	899			2		1153
	IN02			583					583
	IN03	100	95	434					629
	IN04		578	479					1057
	IN05		3	568			4		575
	IN06	1	300	420					721
	IN07			965					965
	IN08		478	795					1273
	IN09			488					488
	subtotal	101	1706	5631			6		7444
Total		370	4200	13792	73	1647	2923	65	23070

Results

Frequency of WEC by age-stage, INF site, sire breed type

The frequency of records across sites and age stages by sire breed type is shown in Table 1. There were 5,961, 9,665 and 7,444 for Maternal, Merino and Terminal breeds, respectively. Across flocks, except for the minimum number of observations for IN09 (505), there were relatively fewer observations for IN05 (1,759) and IN06 (1,842) and much more observations for IN01 (4,508) and IN08 (4,336) in total across sire breed types. The numbers of observations per year were 3,534, 5,165, 5,632, 4,957, and 3,782 for the years from 2007 to 2011 respectively. As for age stages, 73.4% of animals had one record in P stage and P was the most common age stage for WEC measurement (13,792), the next were: W (4,200), H (2,923), Y (1,647). The frequency distribution of WEC along age at observation (Ageatobs) is shown in Figure 1.
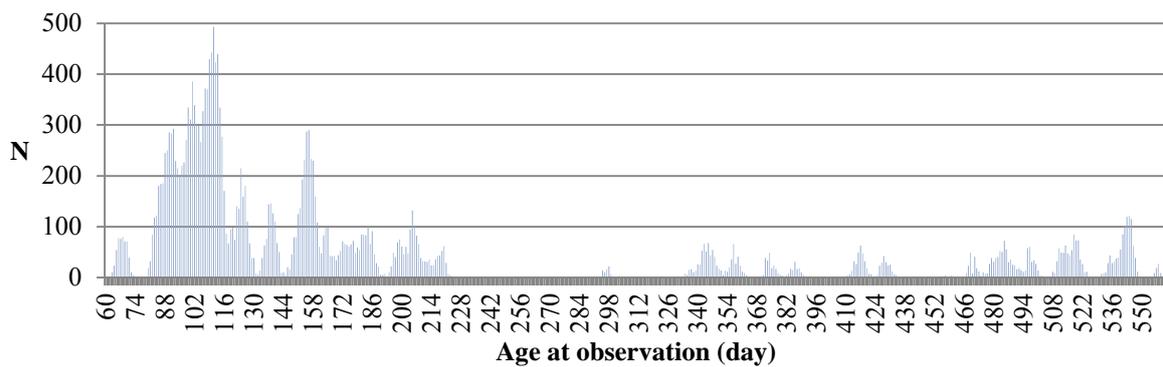
Figure 1. Number of records across age at observation (day)
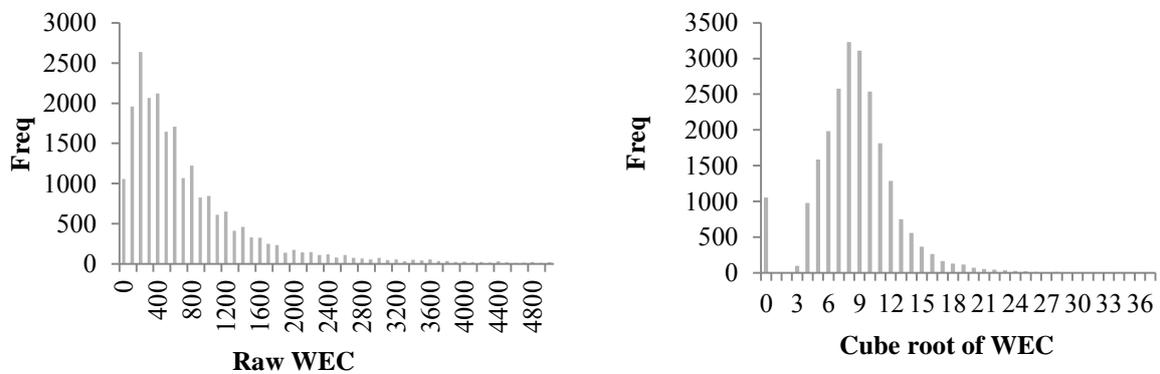
Figure 2. Frequency of raw and cube root transformed WEC
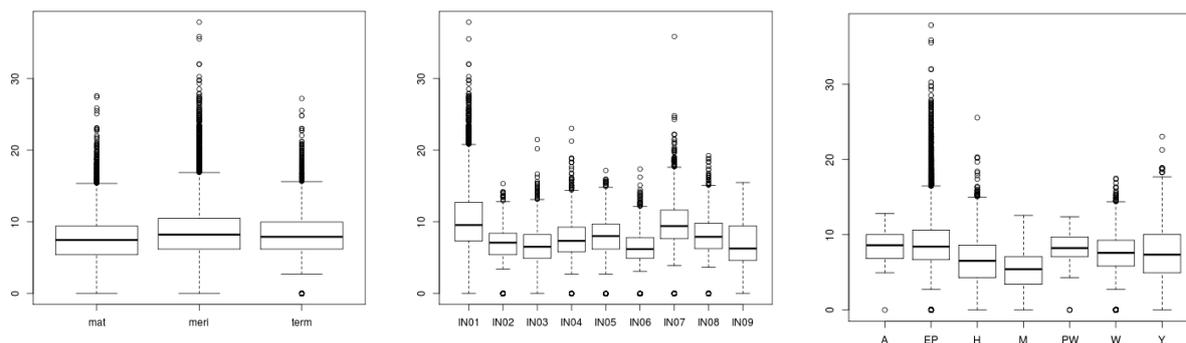
Figure 3. Distribution (box plot) of cube root of WEC by sire breed type (Maternal, Merino and Terminal; Left), flocks (IN01-IN09; Middle), and age stages (Right). The central rectangle spans the first quartile to the third quartile. A segment inside the rectangle shows the median.

Distributions of raw and transformed WEC.

The frequency of raw and transformed WEC (cube root) is shown in Figure 2. The transformed WEC was much normally distributed than the raw WEC and was used in the genetic analyses.

Distributions of WEC by age-stage, INF site, sire breed type

The phenotypic means of three sire breed types were similar. Slightly higher means for IN01and IN07 and slightly lower mean for IN06 were found. As to four age stages, mean of WEC from P was slightly higher than from W, H and A stages (Figure 3).

Genetic parameters by sire breed type

Genetic groups in the pedigree file had very little effect on the estimates of heritability across all four age stages (estimates not shown here).

All three sire breed types have similar trend of phenotypic variances across age stages, which were lower at W and P stages (range of 5.6 to 7.1) and higher at Y and H stages (range of 8.1 to 10.4). Heritability estimates varied across age stages with a range of 0.18 to 0.36 and 0.11 to 0.28 for models with and without SBF respectively for the full dataset (combining all sire breed types) (Table 2). Heritability estimates were relatively consistent across stages for Merinos, ranging from 0.20 to 0.35 for models without SBF and from 0.13 to 0.25 for models with SBF. Much higher heritability estimates (range of 0.44 to 0.77) for Maternal for most stages except for P stage (without SBF: 0.19, with SBF: 0.15) were obtained. It may be due to limited number of observation available for the Maternal sire breed (405 for yearling, 1,063 for weaning stage, and 1,226 for hogget stage). For Terminal sire breed, there were no observations available for Y and H stages and heritability estimates were 0.21 (W) and 0.18 (P) from models without SBF and was 0.11 from models with SBF.

As most of observations were recorded at P stage, heritability estimates for P stage across three sire breed types were more consistent than other stages, ranging from 0.18 to 0.20 without SBF in the models and from 0.11 to 0.15 with SBF in the models.

Table 2. Basic statistics, estimates of phenotypic variance (σ^2_p), heritability(h^2), proportions of SBF variance to the phenotypic variance (sf^2) for the full dataset and subsets (All sire breed types, Merino, Maternal and Terminal) for WEC at four stages (W, P, Y and H) as different traits from analyses without 87 genetic groups in the pedigree file.

dataset	stage	N	mean	std	min	max	sf	σ^2_p	se	h^2	se	sf^2	se
All	W	4200	7.3	2.8	0	17.5	-	6.4	0.15	0.34	0.04	-	-
							+	6.4	0.15	0.20	0.05	0.08	0.02
	P	13792	8.5	4.0	0	38.0	-	6.3	0.08	0.22	0.02	-	-
							+	6.3	0.08	0.15	0.02	0.05	0.01
	Y	1647	7.0	4.1	0	23.1	-	8.7	0.32	0.36	0.07	-	-
							+	8.7	0.32	0.28	0.09	0.04	0.03
	H	2923	6.4	3.6	0	25.7	-	10.1	0.29	0.33	0.05	-	-
							+	10.1	0.28	0.21	0.06	0.06	0.02
Merino	W	1431	8.0	2.8	0	17.5	-	6.8	0.27	0.33	0.08	-	-
							+	6.8	0.27	0.25	0.09	0.04	0.03
	P	5048	9.3	4.5	0	38.0	-	6.9	0.15	0.20	0.03	-	-
							+	6.9	0.15	0.13	0.04	0.05	0.01
	Y	1242	7.3	4.0	0	23.1	-	8.1	0.34	0.35	0.09	-	-
							+	8.1	0.34	0.23	0.12	0.05	0.03
	H	1691	6.8	3.6	0	25.7	-	10.4	0.38	0.28	0.07	-	-
							+	10.3	0.38	0.15	0.08	0.07	0.03
Maternal	W	1063	6.9	2.8	0	15.4	-	7.0	0.38	0.77	0.11	-	-
							+	7.1	0.41	0.56	0.14	0.13	0.04
	P	3113	8.2	3.6	0	27.6	-	5.9	0.16	0.19	0.05	-	-
							+	5.9	0.16	0.15	0.05	0.03	0.02
	Y	405	5.9	4.2	0	18.8	-	10.3	0.81	0.61	0.18	-	-
							+	10.3	0.81	0.52	0.26	0.03	0.07
	H	1226	5.8	3.4	0	15.9	-	9.6	0.43	0.44	0.10	-	-
							+	9.6	0.43	0.44	0.10	0.00	0.00
Terminal	W	1706	7.0	2.7	0	16.4	-	5.8	0.21	0.21	0.06	-	-
							+	5.8	0.21	0.11	0.08	0.06	0.03
	P	5631	8.0	3.5	0	27.3	-	5.6	0.11	0.18	0.03	-	-
							+	5.6	0.11	0.11	0.03	0.05	0.01
	Y	x	x	x	x	x	-	x	x	x	x	x	x
							+	x	x	x	x	x	x
	H	x	x	x	x	x	-	x	x	x	x	x	x
							+	x	x	x	x	x	x

Note: x means no enough data to get ASReml run for the analyses.

Genetic parameters by age of animal

Results from MT method

The phenotypic variances and heritability estimates with SBF and without SBF for age stages and

genetic correlations among 4 age stages were shown in Table 3. Higher phenotypic variances were estimated for H (10.05) and Y (8.58) stages in which less observations were available. Lower similar variances were estimated for W (6.30) and P (6.34) stages with more observations. The heritability estimates were between 0.23 and 0.36 without SBF in the models and were between 0.17 and 0.26 with SBF in the models across age stages. The moderate genetic correlations were found between four age stages, ranging from 0.32 to 0.61 when SBF effects were not taken into account in the models. However, much higher genetic correlations (range of 0.46 to 0.90) were obtained when SBF effects were fitted in the models. Moderate phenotypic correlations were presented only between H and W along with H and Y stages. All other phenotypic correlations were weakly related.

Table 3. Estimates of phenotypic variance (σ^2_p), heritability (h^2), genetic (below diagonal) and phenotypic correlation (above diagonal) for WEC of four age stages from models without SBF (a) and with SBF (b) using data combining all sire breed types (s.e. in subscript)

a) Without SBF

	Wwec	Pwec	Ywec	Hwec
σ^2_p	$6.34_{0.15}$	$6.30_{0.08}$	$8.58_{0.32}$	$10.05_{0.28}$
h^2	$0.36_{0.04}$	$0.23_{0.02}$	$0.34_{0.07}$	$0.29_{0.05}$
Wwec		$0.19_{0.03}$	$0.20_{0.05}$	$0.49_{0.21}$
Pwec	$0.53_{0.09}$		$0.11_{0.03}$	$0.04_{0.02}$
Ywec	$0.51_{0.14}$	$0.32_{0.12}$		$0.56_{0.67}$
Hwec	$0.50_{0.16}$	$0.46_{0.10}$	$0.61_{0.17}$	

b) With SBF

	Wwec	Pwec	Ywec	Hwec
σ^2_p	$6.37_{0.16}$	$6.30_{0.08}$	$8.57_{0.32}$	$10.04_{0.28}$
h^2	$0.23_{0.05}$	$0.17_{0.02}$	$0.26_{0.09}$	$0.17_{0.06}$
Wwec		$0.20_{0.03}$	$0.20_{0.04}$	$0.44_{0.22}$
Pwec	$0.81_{0.15}$		$0.10_{0.03}$	$0.05_{0.02}$
Ywec	$0.71_{0.22}$	$0.46_{0.17}$		$0.53_{0.72}$
Hwec	$0.90_{0.28}$	$0.69_{0.17}$	$0.89_{0.30}$	

The data structure in terms of the number of animals and sires with observations across age stages were shown in Table 4. There were very few animals with observations measured at both W and P stages, W and H stages as well as Y and H stages. But the number of common sires with progeny measured across different stages ranged from 121 (W and H) to 293 (W and P). The standard errors of genetic correlations were related to the number of observations, number of animals and number of common sires for both traits. For example, the lowest standard error of 0.09 for genetic correlation between W and P stages (without SBF) was from most recorded stages and most of common sires (293) though there was no animal with both traits recorded.

Table 4. Number of animals (N_{anim}) and sires (N_{sire}) with observations as well as number of animals (above diagonal) and sire (below diagonal) with observations recorded across four age stages for the full dataset

	Wwec	Pwec	Ywec	Hwec
N_{anim}	4200	13778	1647	2923
N_{sire}	318	480	220	224
Wwec		0	459	15
Pwec	293		1157	2393
Ywec	150	220		1
Hwec	121	224	152	

Results from random regression method

Results from the third-order Legendre polynomial random regression analyses were most sensible and therefore are presented in this report. The three models (homogenous residuals, heterogeneous residuals and heterogeneous residuals + SBF) had similar trend of heritability estimates along the age of animal (from 90 to 520 days, Figure 4). The heritability estimates were lowest at all ages from the model with heterogeneous error and SBF, which was 0.16 at 90 day and decreased to 0.09 at 120 day, following a slowly increase to 0.32 at 410 day, and then decreased afterwards to 0.24 at 520 day. Heritability from the model with heterogeneous error without SBF was more stable across ages with higher before the 220 day point and lower afterwards compared to the estimates from the model with homogeneous error. The trend observed from random regression analyses is similar to estimates found in the univariate analyses by age stages.
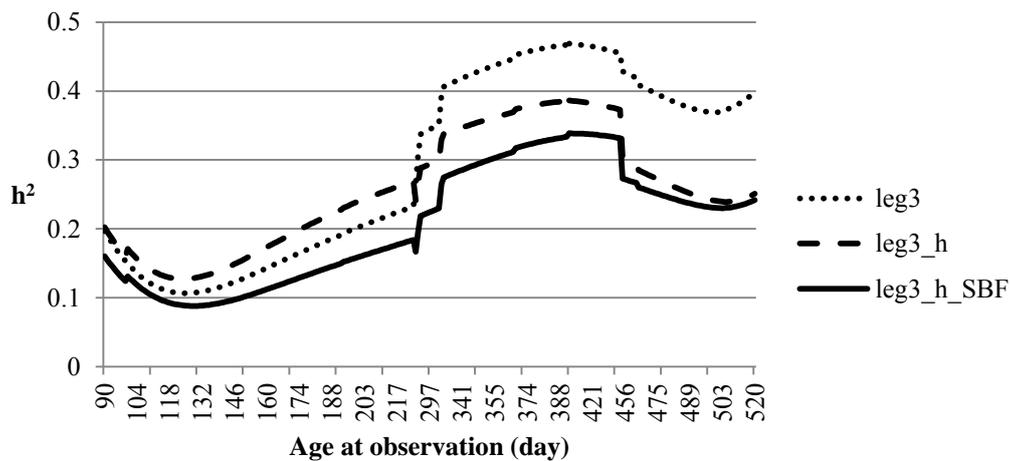
Figure 4. Estimated heritability of WEC as function of the age at observation from the third-order Legendre polynomials random regression analyses with the full dataset by fitting homogeneous error without SBF (leg3), heterogeneous error without SBF (leg3_h) and heterogeneous error with SBF (leg3_h_SBF)

In order to compare genetic correlations from the MT method with results from RR analyses, genetic correlations between age of 100, 136, 373 and 523 days (which are the average age of W, P, Y and H stages) from third-order polynomial random regression with SBF and without SBF are shown in Table 6. Genetic correlations between ages didn't differ significantly between models with SBF and without SBF in RR analyses, but they do differ significantly from those estimated from the MT method. Most of genetic correlation estimates from RR analyses were similar to estimates from the MT model (without SBF) except for much lower correlation of 0.22 between 373 and 523 day comparing to 0.61 between Y and H stage from in MT method . It could be due to limited data to get accurate estimates for those age periods.

Table 6. Genetic correlations between ages days from the third-order Legendre polynomials random regression analyses fitting homogeneous error variance with SBF (above diagonal) and without SBF (below diagonal) by using all three sire type data.

Age, d	100	136	373	523
100		0.70	0.49	0.40
136	0.68		0.39	0.17
373	0.44	0.39		0.25
523	0.46	0.28	0.22	

Genetic correlations between INF sites

Heritability estimates were relatively lower in IN01 (0.20), IN03 (0.19), IN05 (0.11) and higher in IN02 (0.33), IN04 (0.29), IN06 (0.30), IN07 (0.37) and IN08 (0.34) from the analyses using data from W and P stages combing all sire breed types (Table 5). Phenotypic variances varied across flocks, ranging from 2.35 to 11.80 most likely due to the variable contributions of Barber Pole worm across sites.

Table 5. Estimates of phenotypic variance (σ^2_p), heritability (h^2), number of animals (N_{anim}) and sires (N_{sire}) with observations, genetic correlations without SBF (below diagonal) and phenotypic correlations (above diagonal) among 8 flocks using data from P and W stages combining all sire types (s.e. in subscript)

	IN01[*]	IN02	IN03	IN04	IN05	IN06	IN07	IN08
σ^2_p	$11.80_{0.34}$	$4.41_{0.18}$	$5.82_{0.26}$	$2.35_{0.12}$	$3.67_{0.15}$	$5.58_{0.27}$	$5.46_{0.17}$	$5.62_{0.17}$
h^2	$0.20_{0.03}$	$0.33_{0.06}$	$0.19_{0.05}$	$0.29_{0.07}$	$0.11_{0.04}$	$0.30_{0.07}$	$0.37_{0.05}$	$0.34_{0.04}$
IN01		$0.06_{0.07}$	$0.07_{0.09}$	$0.10_{0.08}$	$0.14_{0.06}$	$0.05_{0.08}$	$0.02_{0.06}$	$0.13_{0.06}$
IN02	$0.25_{0.28}$		-	-	$0.15_{0.12}$	$0.23_{0.13}$	$0.07_{0.10}$	$0.11_{0.09}$
IN03	$0.36_{0.44}$	-		-	-	-	$0.14_{0.09}$	$0.11_{0.07}$
IN04	$0.42_{0.33}$	-	-		$0.17_{0.10}$	$0.05_{0.12}$	$0.24_{0.09}$	$0.15_{0.11}$
IN05	$0.93_{0.45}$	$0.79_{0.61}$	-	$0.90_{0.52}$		$0.15_{0.09}$	$0.18_{0.08}$	$0.08_{0.11}$
IN06	$0.20_{0.31}$	$0.74_{0.41}$	-	$0.17_{0.42}$	$0.83_{0.50}$		$0.18_{0.11}$	$-0.04_{0.10}$
IN07	$0.07_{0.23}$	$0.21_{0.28}$	$0.55_{0.33}$	$0.73_{0.27}$	$0.89_{0.40}$	$0.55_{0.33}$		$0.11_{0.07}$
IN08	$0.50_{0.24}$	$0.34_{0.27}$	$0.42_{0.27}$	$0.49_{0.34}$	$0.40_{0.53}$	$-0.11_{0.30}$	$0.31_{0.20}$	

*Flock sites: IN01: Armidale; IN02: Trangie; IN03: Cowra; IN04: Rutherglen; IN05: Hamilton; IN06: Struan; IN07: Turretfield; IN08: Katanning.

In terms of GxE across flocks, significant SBF effects were found in univariate analyses and accounted for 4-8% of total variances which reduced the heritability estimates by around 14 to 48% compared to the estimates without fitting SBF effects in the models (Table 2). Results from permutation tests of 50 repeats showed that significant SBF effects were not caused by random chance (results not shown here).

Genetic correlations from bivariate analyses differed significantly among flocks from as low as -0.11 to highest of 0.93 with standard errors ranging from 0.24 to 0.61 (Table 5). These variable estimates were most likely due to sizes of data set used in bivariate analyses with the number of observations ranging from 1264 (IN03) to 3711 (IN08) among flocks. As there were no animals with observations more than one flock, the genetic correlations were mainly derived from the genetic link based on the pedigree (common sires). The accuracy of genetic correlation was directly related to the number of common sires with progeny observed between flocks. The lowest standard error of genetic correlation was estimated between IN01 and IN08 which were the two big flocks with most observations (3201 and 3711 respectively with 390 common sires), the correlation of 0.50 (s.e. 0.24) between the two flocks was expected to be most accurate. The phenotypic correlations among flocks were not significant from zero, ranging from -0.04 to 0.24.

Table 6. Number of animals (N_{anim}) and sires (N_{sire}) with observations as well as number of sires with observations recorded among 8 flocks (below diagonal) using data from P and W stages combining all sire breed types

	IN01[*]	IN02	IN03	IN04	IN05	IN06	IN07	IN08
N_{anim}	3201	1479	1264	2201	1333	1839	2454	3711
N_{sire}	415	138	170	239	174	236	235	433
IN01								
IN02	127							
IN03	160	44						
IN04	212	56	73					
IN05	147	46	45	101				
IN06	214	63	70	115	95			
IN07	210	56	78	129	97	108		
IN08	390	132	161	206	143	202	198	

Conclusions

Genetic groups in the pedigree file had no effects on the estimates of heritability.

Heritability estimates differed 1) across sire breed types: the average estimates across age stages were 0.12, 0.17 and 0.43 for Terminal, Merino and Maternal breeds respectively; 2) across age stages: 0.16 for P and 0.21 for W, Y and H stages; 3) across flocks: lower for IN01, IN03 and IN05 (range of 0.11-0.20) and higher in IN02, IN04, IN06, IN07 and IN08 (range of 0.29-0.37).

Both MT and RR methods showed that moderate to high genetic correlations were found between four age stages, ranging from 0.32 to 0.61(without SBF) and from 0.46 to 0.90 (with SBF).

Significant SBF effects were found in most of analyses and accounted for 4-8% of total variance and moderate genetic correlations were found between INF sites.

The SBF effects and correlations between flocks significantly lower than 1.0 suggest there is GxE for WEC traits between INF sites.

Because limited observations for some breeds, flocks and age stages, it is necessary to re-analyse some estimates when more data are available.