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Sensitivity of the breeding values for growth rate and worm egg count to environmental worm burden in Australian Merino sheep

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Abstract

The objective of this study was to explore the sensitivity of breeding values for growth rate and worm egg count (WEC, cube root transformed) to environmental worm burden, measured as the average WEC for each contemporary group (CGWEC). Growth rate and WEC were measured on 7,818 naturally infected Merino lambs in eight flocks across Australia, linked through common use of AI sires. Through bivariate analysis, genetic correlations of 0.55 ± 0.23 and 0.30 ± 0.16 were found for growth rate and WEC between low and high CGWEC, respectively. In a second analysis, breeding values for growth rate and WEC were regressed on CGWEC with a random regression model. The heritability for growth rate varied from 0.23 to 0.16 from low to high CGWEC, and the heritability for WEC varied from 0.25 to 0.36. Results suggest that breeding values for both growth rate and WEC are sensitive to environmental worm burden. Animals expressed less genetic variation for growth rate and more genetic variation for WEC in high CGWEC than in low CGWEC. This form of genotype-by-environment interaction should therefore be considered in genetic evaluation of both growth rate and WEC, to increase the efficiency of selection for animals that are more parasite resistant and more resilient to environmental worm challenge.

KEYWORDS

environmental mean, faecal egg count, gastrointestinal nematode infection, tolerance

1 | INTRODUCTION

Sheep production is an important livestock sector in Australia. The production of sheep and lamb meat had a combined gross value of $3.3 billion AUD in the year 2014–15, and the production of wool had a gross value of $2.6 billion AUD (Australian Bureau for Statistics, 2015). However, internal parasites are a large threat to these production systems. Economic losses caused by internal parasites due to reduced wool production and a decreased bodyweight are estimated at $342 million AUD per year (Lane, Jubb, Shepherd, Webb-Ware, & Fordyce, 2015). When losses due to treatment and prevention are included, the total economic losses are estimated at $436 million AUD per year (Lane et al., 2015). Another concern regarding internal parasites is reduced animal welfare. Internal parasites are associated with elevated cortisol levels, anaemia and in the worst case death (Fleming, 1997). Lambs especially are susceptible to infection and the consequences of infection.

The conventional treatment against parasite infection is drenching with anthelmintics such as benzimidazole, levamisole and macrocyclic lactone (Besier & Love, 2003). An increased resistance in parasites against anthelmintics and an increase in consumer concern for anthelmintic residue in products have increased the demand for new ways to control internal parasites (Bisset, Morris, McEwan, & Vlassof, 2001). Promising alternatives for drenching include the use of nematophagus fungi to reduce pasture contamination, vaccination against parasites and breeding sheep for resistance against infection (Besier & Love, 2003).

Breeding for resistance in the form of decreased worm egg count (WEC) has proven to be successful, and WEC has a heritability between 0.1 and 0.4 (Safari & Fogarty, 2003). Joint selection for productivity and WEC also leads to animals being selected to be resistant to the consequences of infection, referred to as resilience. One way to measure resilience is to measure growth under worm challenge (Kelly, Kahn, & Walkden-Brown, 2013). Both resistance and resilience are important traits and are likely to be correlated, but also affect WEC via the environment, as excretion of eggs onto the pasture increases the average worm burden, which in turn increases the chance of (re-) infection within a flock (Bishop, 2012). Large GxE effects were found for WEC in the study of Li, Swan, Brown, and van der Werf (2015), where environments were defined by different regions with different worm burdens. Pollott and Greeff (2004a) found that the heritability for WEC was higher under more extreme environmental worm burdens. Not many have looked at genetic variation in ability to maintain production (or growth) under challenging worm environments, which would be a pragmatic measure of resilience.

The objective of this study was to explore the sensitivity of the breeding values for growth rate and WEC to the environmental worm burden. We will use growth rate under infection to measure resilience, while we will use WEC to measure resistance. The average WEC in each contemporary group will be used as a proxy for the environmental worm burden.

2 | MATERIAL AND METHODS

2.1 | Animals and data

Data were collected on sheep from the Information Nucleus Flock (INF), a program by the Australian sheep Cooperative Research Centre (CRC). This program was set up to obtain accurate estimates of genetic parameters for new traits. The program ran for 5 years between 2007 and 2011. Data were collected for eight flocks across Australia, located in Armidale (New South Wales), Trangie (NSW), Cowra (NSW), Rutherglen (Victoria), Hamilton (Vic), Struan (South Australia), Turretfield (SA) and Katanning (Western Australia). All flocks consisted of ~450 ewes mated per year, except the Armidale and Katanning flocks with ~900 ewes each. For the Armidale flock, an additional 909 records were available in 2012. Ewes were artificially inseminated at all sites. Approximately 100 sires were used annually in the Armidale and Katanning flock. In the other flocks, at least 50% of these sires were used. More information on the structure of the INF can be found in Van der Werf, Kinghorn, and Banks (2010).

The sheep were naturally infected with mixed species of internal parasites (*Trichostrongyle* and *Haemonchus* species). WEC samples were only collected for all individual animals in a given flock when the average worm burden of their cohort group exceeded the threshold. This threshold was set to 1,000 eggs per gram faeces (epg) for sites dominated by *Haemonchus concortus* (mainly the Armidale and Trangie sites), and to 300–500 epg for sites dominated by *Trichostrongylus colubriformis*, and *T. circumcincta* (mainly at the other sites). The worm eggs were counted using a modified McMaster technique (Whitlock, 1948).

This study focused on the dominant sheep breed in Australia, the Merino. Therefore, only data on purebred Merino lambs were extracted from the database. Moreover, only animals with a record for WEC measured between weaning and postweaning were included (ranging between 60 and 330 days, average 127 days). In addition, animals needed at least one body weight recorded around weaning (between 68 and 119 days old, on average 93 days old) and one body weight record postweaning (between 120 and 329 days old, on average 262 days old). Besides WEC and weight, date of measurement and sex were known for the lambs.

Males were castrated and managed together with females. Contemporary groups were created based on flock (8), year (6) and management group within flock-year at weaning. Data from contemporary groups with less than 20 individuals were removed (88 lambs), and one sire with only one offspring was removed. Outliers, defined as observations deviating more than four standard deviations from the mean, were excluded from the analysis (<1% of records).

Observations on 7,818 lambs, 3,988 castrated males and 3,830 females, were used for analysis. These lambs descended from 295 sires and 4,768 dams. Sires had between 2 and 76 offspring, with a mean of 26.5 offspring per sire. Dams had between one and nine offspring, with a mean of 1.6 offspring per dam. Different subtypes of Merino were present in the data set, sire subtypes included South African Mutton Merino (12), Dohne Merino (28), Poll Merino (123) and Merino (132). Dams were either Poll Merino (148), Research (347) or Merino (4,273). Pedigree information was contained on 23,270 animals born over 20

generations. Animals were assigned to different genetic groups (Westell, Quaas, & Van Vleck, 1988), because animals in the INF base generation (AI sires and ewes) originated from different flocks that were not always well linked. The lambs were assigned to 165 genetic groups. A summary of the data is presented in Table 1.

2.2 | Traits

The trait growth rate (g/day) was calculated as live weight gain between weaning and postweaning divided by the growth period. Only lambs with a growth period of more than 30 days were considered. The trait WEC was not normally distributed and was therefore transformed to the cube root of the number of epg faeces ($epg^{0.33}$). The average WEC for each contemporary group was used as an indicator for environmental worm burden, measured in $epg^{0.33}$ (CGWEC).

The environmental worm burden ranged from 3.6 to 18.2 $epg^{0.33}$, with a mean of 8.7 $epg^{0.33}$ which corresponds to approximately 650 epg. Because of the large variation in environmental worm burden, and to allow an investigation of GxE-interaction in a bivariate analysis, growth rate and WEC were considered in two environments: a low worm environment (CGWEC below 7.9 $epg^{0.33}$) and a high worm environment (CGWEC above 9.1 $epg^{0.33}$). Each environment contained approximately 43% of the total number of observations, removing the 14% of observations that were in contemporary groups with a CGWEC between 7.9 and 9.1 $epg^{0.33}$. There were 3,394 lambs with an observation in the low worm environment and 3,352 lambs with an observation in the high worm environment. From the 295 sires, 215 had offspring in both of these environments. There were significant differences in growth rate between the low worm environment and the high worm environment (Table 2).

2.3 | Fixed effects

A linear model was used in R to find significant fixed effects (R Core Team, 2017). The following variables were found significant ($p < 0.05$) for growth rate and fitted as fixed effects; contemporary group (64 levels), sire type (Merino subtype, four levels), sex (two levels) and birth type (the number of lambs per dam at birth, five levels). Weaning age and postweaning age were also tested as fixed effects, but were found not to be significant. Sex by contemporary group interaction was not tested because castrated males and females were managed in the same group.

The following variables were found significant for WEC and fitted as fixed effects: contemporary group, sex, birth type and rearing type (the litter size at weaning, four levels). Age at WEC measurement and weaning age were fitted as covariates. Age of dam was also tested, but was found not to be significant.

2.4 | Univariate analysis

To estimate overall genetic parameters for growth rate and WEC, without regard to environment, we fitted a single trait animal model with ASReml (Gilmour, Gogel, Cullis, & Thompson, 2009). Genetic group of the animal (165 groups), animal and residual were fitted as random variables,

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z_1 a} + \boldsymbol{Z_2 g} + \boldsymbol{e} \quad (1)$$

where $\boldsymbol{y}$ is a vector of observations, $\boldsymbol{X}$ is an incidence matrix for fixed effects ($\boldsymbol{b}$), $\boldsymbol{Z_1}$ and $\boldsymbol{Z_2}$ are the incidence

TABLE 1 Data characteristics for Merino lambs used for analysis

	N	Mean ± *SD*
Birthweight (kg)	7,814	4.68 ± 1.0
Weaning weight (kg)	7,815	24.2 ± 5.2
Postweaning weight (kg)	7,817	37.4 ± 8.2
Weaning age (days)	7,818	93.2 ± 9.7
Postweaning age (days)	7,818	262 ± 45
Growth period (days)[a]	7,743	170 ± 44
WEC age (days)	7,818	127 ± 35
Growth rate (g/day)[b]	7,735	79.9 ± 43
Worm egg count ($epg^{0.33}$)	7,784	8.7 ± 3.8
Contemporary group (number of individuals)	64	122 ± 107
Mean WEC environment (CGWEC, $epg^{0.33}$)	64	8.7 ± 2.8

Notes. [a]Minimum growth period set to 30 days. [b]Growth rate between weaning and postweaning.

TABLE 2 Descriptive statistics for the low and high worm environment, mean ± standard deviation

	Low worm environment	High worm environment
Number of lambs	3,394	3,352
Number of sires	231	276
Number of dams	2,283	2,331
CGWEC range ($epg^{0.33}$)	3.6–7.9	9.2–18.2
Birth weight (kg)	4.7 ± 1.0	4.6 ± 1.0
Weight gain (kg)	13.6 ± 7.6	12.8 ± 6.3
Growth period (days)	169 ± 53	174 ± 33
Growth rate (g/day)	84.7 ± 46	74.0 ± 36
Worm egg count ($epg^{0.33}$)	6.6 ± 2.7	10.9 ± 3.9

matrices relating the records to additive genetic effects ($\boldsymbol{a}$) and genetic group effects ($\boldsymbol{g}$), and e is a vector of residual effects. A maternal genetic effect was found to be non-significant and therefore omitted.

2.5 | Bivariate analysis

To investigate GxE-interaction, a bivariate model was fitted to estimate the genetic correlation between the same trait expressed in the high worm environment and in the low worm environment, that is two separate bivariate models, one for growth rate and one for WEC. The fixed and other random effects were the same as in the univariate analysis. Another bivariate model was used to estimate the genetic correlation between growth rate and WEC, using the full data set.

2.6 | Random regression analysis

To model GxE-interaction in a more continuous manner, a random regression model was fitted with CGWEC as a continuous covariable. This model allowed the random effects to vary over different levels of the environmental worm burden trajectory. The random additive genetic effect of the animal and the random genetic group effects were fitted as a Legendre polynomial function of CGWEC. A Legendre polynomial was also fitted for the fixed effects to allow them to vary across the trajectory of CGWEC. Several orders of polynomial were tested, starting at a first-order fit (linear). The following model was used:

$$\begin{aligned} \boldsymbol{y}_{ij} = \boldsymbol{F_1} + \textstyle\sum_{m=0}^{k_{A-1}} \boldsymbol{F}_{im}\varphi_{\boldsymbol{m}}(\boldsymbol{t}_{ij}) + \sum_{m=0}^{k_{B-1}} \alpha_{im}\varphi_{\boldsymbol{m}}(\boldsymbol{t}_{ij}) \\ + \textstyle\sum_{m=0}^{k_{C-1}} \boldsymbol{g}_{im}\varphi_{\boldsymbol{m}}(\boldsymbol{t}_{ij}) + \varepsilon_{ij} \end{aligned} \quad (2)$$

where $\boldsymbol{t}_{ij}$ is CGWEC for $\boldsymbol{y}_{ij}$, standardized between −1 and 1, the corresponding $\boldsymbol{m}$-th Legendre polynomial $\boldsymbol{\varphi_m}$ ($\boldsymbol{t}_{ij}$), the $\boldsymbol{m}$-th order coefficient for fixed effects $\boldsymbol{F}_{im}$, additive genetic effect $\boldsymbol{\alpha}_{im}$, and genetic group $\boldsymbol{g}_{im}$, $\boldsymbol{k}_{A\text{-}1}$ refers to the $\boldsymbol{k}_A$-th order of polynomial fit for the particular effect, and the residual error $\boldsymbol{\varepsilon}_{ij}$. Heterogeneity of the residual variance was assumed, depending on the CGWEC values, with seven residual variances estimated for the value ranges of 3.6–5, 5–7, 7–9, 9–11, 11–13, 13–15 and 15–18.2 epg$^{0.33}$. The log likelihood ratio test (chi-squared distribution) was used to determine what order polynomial fitted best for each random effect.

For growth rate, a first-order Legendre polynomial was fitted for animal and genetic group. A second-order Legendre polynomial for animal or genetic group did not converge. A third-order Legendre polynomial was fitted for sex. Fitting birth type with a Legendre polynomial did not significantly improve the model and was therefore added as constant across the trajectory. Contemporary group and sire type were also fitted as constant fixed effects ($\boldsymbol{F_1}$).

A first-order Legendre polynomial for animal and genetic group was also fitted for WEC. A model with a second-order Legendre polynomial for animal or genetic group did not converge or did not significantly improve the log likelihood. A first-order Legendre polynomial was also fitted for birth type and rearing type, and a second-order Legendre polynomial was fitted for sex and age of measurement. Contemporary group and weaning age were fitted as regular fixed effects.

Fitting the random regression model results in a matrix of the variances and covariance between the random regression coefficients α_{im}, the so-called $\boldsymbol{K}$ matrix. To find variances at, and covariance between, traits expressed at different worm burdens, matrix $\boldsymbol{K}$ was pre- and postmultiplied with $\boldsymbol{\Lambda}$, where $\boldsymbol{\Lambda}$ contained the Legendre polynomial coefficients for specific values of CGWEC. This resulted in the estimated $\boldsymbol{G}$ matrix, the (co)variance matrix of breeding values at the specific CGWEC values as defined in $\boldsymbol{\Lambda}$,

$$\hat{\boldsymbol{G}} = \Lambda \boldsymbol{K}_{\boldsymbol{A}} \Lambda' \quad (3)$$

2.7 | Comparing genetic parameters

The genetic parameters from the best random regression model were then compared to the genetic parameters from the uni- and bivariate models. To compare the models, genetic parameters were evaluated for three levels of CGWEC: (a) the average CGWEC of the low worm environment; 6.6 epg$^{0.33}$, (b) the average CGWEC for the whole data set; 8.7 epg$^{0.33}$ and (c) the average CGWEC of the high worm environment; 11.0 epg$^{0.33}$. These levels will be referred to as low, mid and high CGWEC, respectively.

3 | RESULTS

3.1 | Data characteristics

As the lambs were naturally infected, few observations were available for contemporary groups with extreme values for CGWEC (Figure 1). Most contemporary groups had a CGWEC between 7.3 epg$^{0.33}$ and 9.3 epg$^{0.33}$.

3.2 | Growth rate

The mean growth rate was 79.9 ± 42.5 g/day. Female lambs grew on average 14 g/day less than male lambs. Lambs from a South African Mutton Merino sire or a Dohne Merino sire had a higher growth rate than lambs from a Poll Merino or Merino sire.

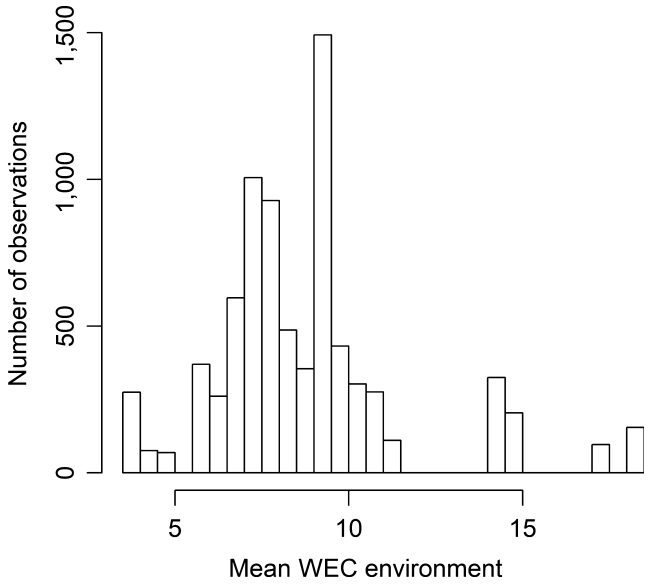

FIGURE 1 The distribution of observations over environmental worm burden (mean worm egg count in each contemporary group, in epg$^{0.33}$)

Overall heritability of growth rate was 0.17 ± 0.03, as estimated from the univariate model (Table 3). From the bivariate model, the estimated heritability for growth rate in the low worm environment (0.35 ± 0.03) was higher than the heritability for growth rate in the high worm environment (0.08 ± 0.03). The genetic correlation between growth rate in the low and high worm environment was 0.55 ± 0.23.

With the random regression model, the additive genetic variance for growth rate showed a steady decrease with increasing CGWEC. The residual variance showed no clear trend. The heritability for growth rate therefore decreased with increased environmental worm burden (Figure 2). The heritability estimates for a low, mid and high CGWEC were 0.23, 0.23 and 0.16, respectively.

TABLE 3 Estimated genetic parameters from the uni- and bivariate models of growth rate and worm egg count

Trait	σ_a^2	σ_p^2	h^2 (*SE*)
Growth rate	149	880	0.17 (0.03)
Growth rate – low[a]	324	925	0.35 (0.03)
Growth rate – high[a]	55.6	685	0.08 (0.03)
Worm egg count	1.33	6.70	0.20 (0.03)
Worm egg count – low[b]	1.16	6.23	0.19 (0.03)
Worm egg count – high[b]	2.83	7.74	0.37 (0.03)

Notes. [a]The estimated genetic correlation between growth rate in the low and high worm environment was 0.55 ± 0.23. [b]The estimated genetic correlation between worm egg count in the low and high worm environment was 0.30 ± 0.16.

With the random regression model, the genetic correlation between growth rates in the two most extreme contemporary groups (CGWEC 3.6 and 18.2 epg$^{0.33}$) was 0.65. The genetic correlations between growth rate at the mean values of the low, mid and high CGWEC were all above 0.99. These high genetic correlations indicate that there was no re-ranking of sires for growth rate between different environmental worm burdens. However, there was a reduction in phenotypic and genetic variance in the high CGWEC environments and therefore a smaller breeding value range. The estimated sire breeding values for growth rate ranged from −28.2 to 34.9 in low CGWEC, and from −19.6 to 23.9 in high CGWEC.

3.3 | Worm egg count

The mean WEC was 8.7 ± 3.8 epg$^{0.33}$. Female lambs had on average a WEC of 0.3 epg$^{0.33}$ lower than male lambs. Lambs with siblings at birth tended to have a higher WEC than singleton lambs. Lambs with siblings at weaning had on average a lower WEC than lambs with no siblings at weaning.

The overall heritability for WEC was 0.20 ± 0.03 as estimated from the univariate analysis and did not differ significantly from the heritability in the low worm environment (0.19 ± 0.03). The heritability in the high worm environment was estimated to be 0.37 ± 0.03 (Table 3). The genetic correlation between WEC in the low and the high worm environment was 0.30 ± 0.16, indicating significant re-ranking of sires between both environments.

With the random regression model, the additive genetic variance for WEC had the lowest value around the mean CGWEC and increased in the more extreme CGWEC. The

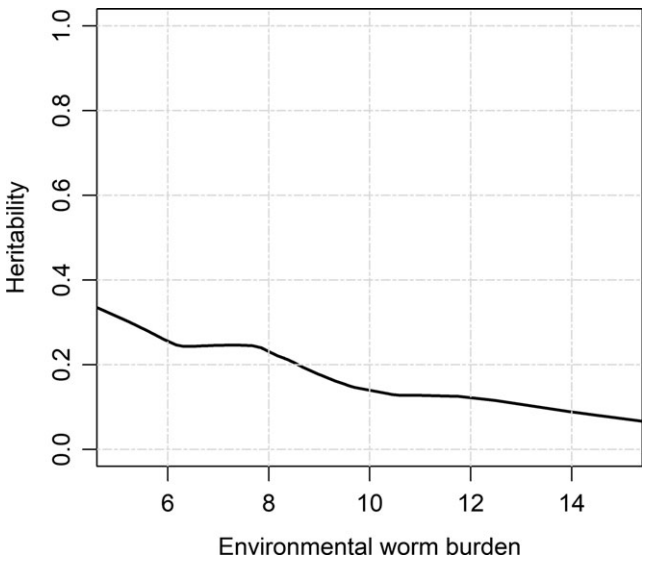

FIGURE 2 The heritability of growth rate over the range of worm burden environments (in epg$^{0.33}$)

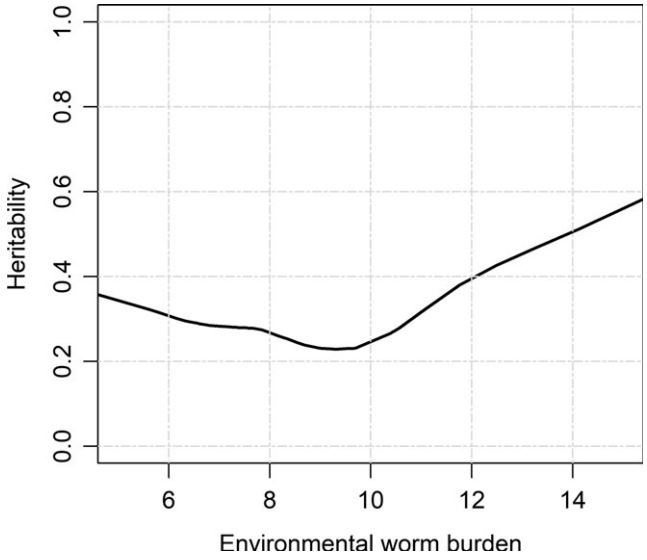

FIGURE 3 The heritability of worm egg count over the range of worm burden environments (in $epg^{0.33}$)

residual variance also increased towards the more extreme CGWEC; however, around the mean level of CGWEC the residual variance also increased slightly. The heritability of WEC is shown over different environmental worm burdens for the final model (Figure 3). The heritability estimates from the random regression model for the low, mid and high CGWEC were 0.25, 0.25 and 0.36, respectively.

With the random regression model, the genetic correlation was 0.83 between the low and mid-CGWEC, and 0.74 between the mid and high CGWEC. The genetic correlation between the low and high CGWEC was 0.24, which indicates significant re-ranking. Figure 4 shows considerable re-ranking of the sire breeding values for the top 5% most accurate sires.

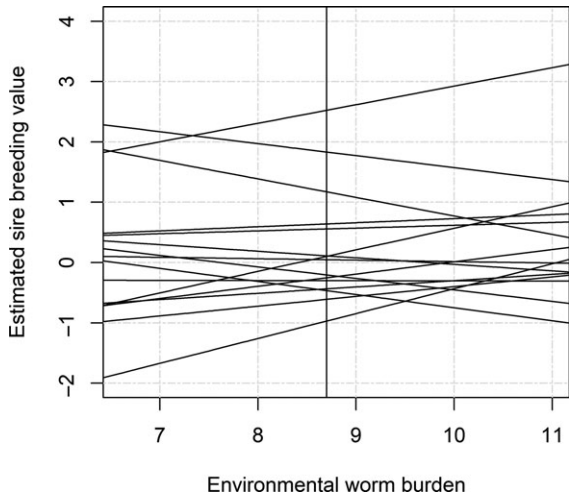

FIGURE 4 Estimated sire breeding values for the top 5% most accurate sires for worm egg count over the range of worm burden environments. Each line represents the EBV of a sire that was used in different worm environments. The vertical line represents the mean environmental worm burden

TABLE 4 Estimated genetic and phenotypic correlations (*SE*) between growth rate and worm egg count in the low, overall and high worm environment

	r_g	r_p
Low worm environment	−0.12 (0.13)	−0.03 (0.02)
Overall worm environment	−0.14 (0.11)	−0.04 (0.01)
High worm environment	0.09 (0.21)	−0.06 (0.02)

3.4 | Genetic correlation between growth rate and worm egg count

A genetic correlation of -0.14 ± 0.11 was found between growth rate and WEC from univariate analysis using the whole data set (Table 4). The corresponding phenotypic correlation was -0.04 ± 0.01. The standard errors were high for all the genetic correlations. The phenotypic correlations between growth rate and WEC were of similar magnitude in all worm environments.

4 | DISCUSSION

In this study, the sensitivity of the breeding values for growth rate and WEC to environmental worm burden (CGWEC) was investigated. Genetic parameters reflecting a genotype-by-environment interaction were estimated from naturally infected lambs in eight flocks across Australia. Results showed that the breeding values for growth rate and WEC are sensitive to environmental worm burden. Growth rate showed a reduced genetic variance in high CGWEC but limited re-ranking of sire breeding values, whereas WEC showed an increased genetic variance in high CGWEC and significant re-ranking between sire breeding values in low CGWEC and high CGWEC.

4.1 | Growth rate

The heritability for growth rate in the low worm environment (0.35 ± 0.03) was significantly higher than the heritability for growth rate in the high worm environment (0.08 ± 0.03), as estimated from the bivariate model. The heritability estimates from the random regression model were more similar, but there was a clear decreasing trend with increasing environmental worm burden. The genetic correlation as estimated from the bivariate model (0.55 ± 0.23) indicated re-ranking of sires. However, genetic correlations estimated between different CGWEC from the random regression model were high (>0.99), indicating that there was no re-ranking between sires in

different environmental worm burdens. In the most extreme case, the genetic correlation from the random regression model was moderate at 0.65. However, due to the low number of observations in more extreme CGWEC, and the extrapolating nature of the polynomials of the random regression model, the estimates in these areas were considered not accurate. More data in environments with a high nematode burden would improve the accuracy of the associated estimated genetic parameters.

It was found that there was less additive genetic variation for growth rate in a high worm environment, which is of importance because the difference between the best and the worst sires will become less visible. There was a clear reduction in the range of the estimated breeding values of sires. This indicates that animals in the high worm environment are not able to show their genetic potential for growth the same way as animals in the low worm environment. In breeding programmes, this could mean that the genetic gain in high CGWEC is lower than would be expected based on EBVs estimated across all CGWEC environments without accounting for GxE-interaction.

4.2 | Worm egg count

Also for WEC, there was evidence of sensitivity to environmental worm burden. The heritabilities estimated from the bivariate model were significantly different between the low worm environment and the high worm environment. From the random regression model, the estimated heritabilities showed less difference even though the heritability seemed to increase at the more extreme CGWEC. These outcomes are consistent with the results of Pollott and Greeff (2004a), who found that the heritability for WEC increased towards more extreme mean WEC environments. The overall heritability of WEC in their study (0.24) was of similar magnitude as the heritability found in this study. The genetic correlation between the low and high worm environment from the bivariate model (0.30 ± 0.16) indicated that breeding values differed considerably between these environments, that is, resistance in low and high WEC environments is genetically not the same trait. The genetic correlation estimated from the random regression model was similar (0.24).

The low to moderate genetic correlations that were found between low and high CGWEC (0.24), and mid and high CGWEC (0.74), indicate that the best sire in the low worm environment is not necessarily the best sire in the high worm environment. This could mean that genetic evaluation does not always result in the optimal sires to reduce WEC, thereby undermining the genetic gain for this trait. In particular, in areas where worms are a major issue, more efficient selection methods would be beneficial. Genotype-by-environment interaction regarding worm environment should therefore be considered in breeding programmes, to generate more accurate genetic evaluations for parasite resistance.

4.3 | Within flock analysis

Closer inspection of the distribution of flocks over the low and high worm environment revealed that one site in particular (Kirby farm) had a high environmental worm burden. The Kirby farm is located in Armidale, New England, which is known for summer predominant rainfall and a dominance of *H. concortus*, giving higher WECs. High genetic correlations (0.71 and 0.56, 0.87) have been found between WEC of natural infected ewes and WEC of experimentally infected rams (Aguerre et al., 2018; Gruner, Bouix, & Brunel, 2004). Indicating that resistance to single species experimental or mixed natural infection has a similar genetic basis.

While sires were used across all flocks, the ewes at Kirby were more closely related to the local sheep population. The New England region is known for fine to superfine Merino wool sheep that are generally small in stature compared to the average Merino ewe. The analysis accounted for genetic groups to account for differences between merino substrains, although Swan, Brown, and Van der Werf (2015) found that the variation between different substrains of Merino was only small. Further analysis of data from the Kirby site compared to the full population (Table 5) showed that at this site the mean growth rate was lower (71.57 ± 36.27 g/day versus 79.9 ± 42.51 g/day overall) and mean WEC was higher (10.66 ± 4.34 $epg^{0.33}$ versus 8.7 ± 3.79 $epg^{0.33}$ overall). The heritability for growth rate at Kirby was slightly lower compared to all other sites (0.14 ± 0.05 versus 0.17 ± 0.03 overall), and the heritability for WEC was slightly higher (0.25 ± 0.06 versus 0.20 ± 0.03 overall).

TABLE 5 Mean growth rate and worm egg count for the overall data, and for each flock

	Growth rate		Worm egg count	
	Count	Mean ± *SD*	Count	Mean ± *SD*
Overall	7,735	79.9 ± 43	7,784	8.70 ± 3.8
Armidale (Kirby)	2,325	71.6 ± 36	2,292	10.7 ± 4.3
Trangie	646	121 ± 40	647	5.96 ± 2.8
Cowra	549	109 ± 42	549	6.87 ± 2.8
Rutherglen	803	72.6 ± 43	810	7.66 ± 2.6
Hamilton	468	93.6 ± 36	468	8.39 ± 3.0
Struan	602	71.9 ± 45	670	6.61 ± 3.0
Turretfield	985	78.8 ± 39	988	10.7 ± 3.1
Katanning	1,357	66.8 ± 39	1,360	7.80 ± 2.7

To investigate the impact of Kirby farm on the outcome of the analysis, a random regression model was fitted for both traits using a subset of the data without the Kirby site. This analysis revealed that the genetic correlations for both traits between different CGWEC were of similar magnitude as found with the full data set, suggesting that genetic group accounted for differences between flocks. The heritability estimates increased slightly, but the same trends were visible with a higher heritability for WEC and lower heritability for growth rate in high CGWEC. These results are consistent with the study of Li et al. (2015), who found significant GxE-interaction for WEC between the different flocks in the INF. It was concluded that inclusion of the Kirby site had little effect on the outcome of the analysis.

4.4 | Genetic correlation between growth rate and worm egg count

The genetic correlation between growth rate (or other performance traits) and WEC has been studied extensively. In this study, the genetic correlation between growth rate and WEC was not significantly different from zero (-0.14 ± 0.11). This is in agreement with Pollott and Greeff (2004b), where nonsignificant genetic correlations of −0.06 and −0.09 were found between live weight and WEC, and with Brown and Fogarty (2017), who found nonsignificant genetic correlations between these traits ranging between 0.00 and 0.05. However, it contrasts with Pollott, Karlsson, Eady, and Greeff (2004), who found an overall genetic correlation of 0.32 between body weight and WEC, and Bishop, Bairden, McKellar, Park, and Stear (1996) who found genetic correlations between weight gain and WEC ranging from −0.63 to −1.00. It appears that the genetic correlation between growth rate and WEC is not consistent across studies. Further research is needed to better understand the relationship between WEC and growth rate.

5 | CONCLUSION

Our results show that the breeding values for growth rate and WEC are sensitive to environmental worm burden. For growth rate, the additive genetic variance decreased with increasing environmental worm burden, making it harder to distinguish the best from the worst sires in high worm environments. This could mean that genetic gain for growth rate is lower than expected in high worm environments. For WEC, re-ranking of sire breeding values was visible between low and high environmental worm burden, indicating that the best animal in low environmental worm burden is not necessarily the best animal in high environmental worm burden. This could undermine the genetic gain for this trait. Based on these findings, we suggest that consideration should be given in the genetic evaluation of both growth rate and WEC to account for this form of genotype-by-environment interaction. In practice, it is also important that sires used in high worm burden environments have also been tested in such environments, both for WEC as for growth traits.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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