Correlated responses following genetic selection to change faecal worm egg count in Romney sheep

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ABSTRACT

Genetic studies of nematode parasite-related traits were carried out in New Zealand Romney sheep between 1979 and 2006. Breeding lines were selected for high or low faecal worm egg count (FEC), and managed alongside a control unselected line. FEC data were collected from lambs post-weaning, whilst exposed to continuous, natural, mixed-species, nematode parasite challenge under grazing conditions. Overall there were 33,314 records of lamb FEC, taken at 'FEC1' and 'FEC2' (first and second post-weaning sampling times, separated by a drench treatment). Genetic parameter estimates are reviewed, including correlations of FEC with lamb, anti-parasite antibody and ewe performance traits. The heritability of FEC in lambs was 0.26 ± 0.01 overall, with a repeatability of 0.40 ± 0.01. The genetic correlation between FEC1 and FEC2 was 0.85 ± 0.02. Trends were for low FEC to be associated genetically with slight reductions in post-weaning growth, and in ewe and lamb fleece weights, minimal change in autumn and yearling live weights, and increased weaning weight, dag score and anti-parasite antibody levels. In practice, ram breeders would normally use index selection procedures, to achieve higher production at the same time as a lower FEC, although a slower rate of change in FEC would be expected.

Keywords: sheep; resistance; selection; nematode parasite; genetic.

INTRODUCTION

Breeding for host resistance to nematode parasites in sheep offers farmers an alternative opportunity for more sustainable animal production. By using breeding strategies, farmers can address issues such as populations of parasites increasingly resistant to anthelmintics and consumer demand for reduced chemical inputs, ultimately reducing the overall cost of drenching. Single-trait experimental breeding lines of Romney sheep were selected for resistance or susceptibility to nematode parasites by Ministry of Agriculture and Fisheries/AgResearch staff for nearly 30 years. A number of publications have documented the selection responses over time (Douch *et al*., 1995; Bisset *et al*. 1996; Morris *et al*., 1997, 2000; Wheeler *et al.*, 2008), and summarised the genetic parameters obtained in these lines (Morris *et al*., 1998, 2004a). This report brings together the main results obtained in Romney sheep.

MATERIALS AND METHODS

Ethics

This work was carried out with the approval of the AgResearch Ruakura, Wallaceville and Grasslands Animal Ethics Committees.

Selection lines

Breeding lines selected exclusively for high or low resistance to nematode infection, measured in lambs post-weaning using faecal egg count (FEC), were established and maintained at Wallaceville from 1979, and at Rotomahana from 1985. Prospective parents with the lowest breeding values (BV) for low FEC as described below, were used in the Low-FEC line, and those with the highest BV for FEC in the High-FEC line. The Wallaceville and Rotomahana lines were merged in 1993 (Morris *et al*., 2000), forming a combined High line and a combined Low line. These two lines were subsequently maintained alongside a Control unselected line until the 2006 lamb crop. It was known from early post-mortem studies that genetically selecting live animals on FEC would lead to significant differences in worm burdens of the majority of economically important nematode parasite species (Bisset *et al*., 1996). A progeny-test flock of Romneys was grazed initially alongside the selection lines, providing reference sires, and also larger numbers of progeny for the evaluation of potential young sires. Another Romney line, selected for the ability to maintain acceptable health and growth under parasite challenge, with minimal need for anthelmintic treatment, termed resilience, was set up in 1994. This line was also grazed mainly at Wallaceville and Ballantrae (see Bisset *et al*. (2001) and Wheeler *et al.* (2008)), and reference-sire links to the FEC lines were maintained via the progeny-test flock mentioned above. FEC data from all the above resources were used in the present genetic analyses.

Animal recording and sampling

Weaning weight was taken at about 90 days of age, generally in December, and an anthelmintic drench treatment was administered at this stage. The primary trait in the FEC selection lines was FEC measured on two faecal samples from lambs post-weaning. This was a combination of FEC1, generally taken in January/February, and FEC2, generally taken in March/April. All animals were sampled when the mean FEC of a monitor group of lambs reached 1,000 to 1,500 eggs/g. A drench treatment was administered immediately after the FEC1 sampling, thus ensuring that FEC1 and FEC2 represented separate infections. Faecal samples were also collected from peri-partum ewes, sampled on repeated occasions within season when no drench was administered between samplings, and between seasons.

Serum antibody levels to *Trichostrongylus colubriformis* third larval stage antigens were obtained from selection-line lambs post-weaning from the 1989-91 lamb crops, providing anti-*T. colubriformis* immunoglobulin (Ig-Tc), and also IgG_1 and IgE data (Douch *et al*., 1995; Shaw *et al*., 1999). Serum IgE responses to nematode aspartyl protease inhibitor (IgE-Aspin) were also obtained, as reported by Shaw *et al*. (2003). In later lamb crops from the 2003 birth year onwards, saliva samples were collected from lambs post-weaning, for measurement of the IgA antibody to a nematode carbohydrate larval antigen (CarLA) (R.J. Shaw, Unpublished data). On account of limited numbers of selection-line animals sampled for the CarLA-saliva assay, the correlations of FEC with CarLA presented in this review were obtained from a wider source of animals consisting of 12 industry flocks (2007 birth-year lambs).

Resilience in experimental lambs after weaning was measured as age at first drench, within grazing group, using individual drench-as-required information as described by Bisset *et al*. (1994). More resilient animals were thus older at first drench.

Sample analysis

Eggs of *Nematodirus* spp. (NEM) were recorded separately from those of other strongyle nematodes when measuring FEC. Both types of eggs were counted using a modified McMaster technique, in which each egg counted represented 100 eggs per gram of faeces. Genetic parameters involving NEM in this paper are taken from analyses carried out on the 1979 to 2000 lamb crops (Morris *et al*., 2004a). Those involving ewe FEC were taken over six lambing seasons between 1987 and 1996 (Morris *et al*., 1998).

Ig-Tc, IgG_1 and IgE concentrations from blood samples were analysed by ELISA (Shaw *et al*., 1999), expressed as optical density units by reference to a standard, as was IgE-Aspin concentration (Shaw *et al*., 2003). CarLA specific-IgA concentrations from saliva samples were measured using an ELISA method (Ramírez-Restrepo *et al*., 2010), with results calculated from a standard curve and expressed in units/mL. The lower limit for CarLA IgA data was set at 0.3 units/mL, representing the minimal detectable limit of the assay, which was relevant for the scale transformation.

Statistical analysis

The complete set of FEC1 and FEC2 data comprised 33,314 records. FEC, NEM, antibody concentrations and CarLA IgA concentrations were transformed to natural logarithms, to normalise their distributions for analysis.

The traits analysed in this report were weaning weight, post-weaning gain (January to autumn (March/April)), $\log_e$(FEC + 100), $\log_e$(NEM + 100), breech soiling as measured by dag score (0 = No dags, to 4 = Heavy dags), autumn weight, $\log_e$Ig-Tc and $\log_e$CarLA-IgA. All of these traits were recorded in both sexes. In addition ewe yearling weight, ewe yearling fleece weight and ewe fleece weight were recorded. Ewe litter size as number of lambs born per ewe lambing, was also analysed, using data from the FEC selection and control lines.

All parasite and production traits were analysed using repeated-records animal model restricted maximum likelihood (REML) procedures (Gilmour *et al.*, 2002), with a full relationship matrix. Selection line was not fitted, because this was accounted for with the relationship matrix. Fixed effects in the models were year of birth, sample time and contemporary group, with the latter accounting for combinations of grazing group and sex of lamb. Three-trait and four-trait models were used, including $\log_e$(FEC1+100), $\log_e$(FEC2+100) and up to two other lamb traits at the same time. Log_e(FEC+100) as a lamb was analysed with each of lamb dag score, ewe fleece weight and litter size as second traits, treating each pair of traits as repeated records.

RESULTS

The net results of single-trait selection in the Wallaceville lines on FEC as a heritable trait for over 25 years were differences between the Control-FEC and Low-FEC line in FEC by factors of 6.3 for both sexes in February, and 13.6 for females in April. Similar multiplicative differences were also observed between the High-FEC and Control lines.

Log_e-transformed FEC from lambs had a heritability estimate of 0.26 ± 0.01, with a repeatability of 0.40 ± 0.01. Treating transformed FEC1 and FEC2 as two separate traits led to heritabilities of 0.25 ± 0.01 and 0.33 ± 0.02, respectively, and a genetic correlation between them

TABLE 1: Phenotypic and genetic correlations between faecal egg count (log_eFEC + 100) and either production traits or antibody responses.

Characterisitcs	Phenotypic correlation		Genetic correlation	
	loge (FEC1 + 100)	loge (FEC2 + 100)	loge (FEC1 + 100)	loge (FEC2 + 100)
Weaning weight	-0.06± 0.01**	-0.02 ± 0.01	-0.11 ± 0.04**	-0.05 ± 0.04
Post-weaning weight gain1	-0.03 ± 0.01**	-0.11 ± 0.01**	0.06 ± 0.05	0.01 ± 0.05
Autumn live weight	-0.08 ± 0.01**	-0.08 ± 0.01**	-0.02 ± 0.04	-0.01 ± 0.04
Yearling live weight	-0.06 ± 0.02**	-0.07 ± 0.02**	-0.00 ± 0.05	-0.06 ± 0.05
Hogget fleece weight	-0.02 ± 0.02	-0.01 ± 0.02	0.17 ± 0.05**	0.13 ± 0.05*
Ewe fleece weight	0.02 ± 0.02		0.07 ± 0.05	
Ewe litter size	-0.01 ± 0.01		-0.01 ± 0.08	
Lamb dag score	-0.04 ± 0.01**		-0.12 ± 0.04**	
Serum Ig-Tc2 concentration	-0.14 ± 0.03**		-0.47 ± 0.15**	
Saliva CarLA IgA3 concentration	-0.10 ± 0.03**		-0.49 ± 0.07**	
Lamb resilience	-0.10 ± 0.02**		-0.00 ± 0.08	

[1]January to March/April
[2]Antibody to *T. colubriformis*. Similar results also from IgG_1, IgE and IgE-Aspin (Shaw *et al.*, 1999, 2003)
[3]CarLA IgA results from industry flock data in 2008.

of 0.85 ± 0.02. For *Nematodirus*, corresponding heritability estimates for log_e-transformed NEM1 and NEM2 were 0.15 ± 0.03 and 0.26 ± 0.04, with a phenotypic correlation of 0.24 ± 0.02 and a genetic correlation of 0.85 ± 0.08. The genetic correlation between log_e(NEM+100) and log_e(FEC+100), combined over two post-weaning sampling times was 0.43 ± 0.04. In ewes, the heritability estimate for transformed FEC was 0.37 ± 0.06, with a repeatability over time of 0.46 ± 0.03. The genetic correlation between a ewe's transformed FEC and her transformed FEC as a lamb was estimated to be 0.70 ± 0.08.

Table 1 reviews the phenotypic and genetic correlations between transformed FEC1 or FEC2 and production or antibody traits in experimental Romney sheep, apart from the CarLA IgA values, obtained from industry flocks. Phenotypic correlations between FEC and production traits were generally favourable in sign, with the exception of dag score. Over half of the estimates were significant ($P < 0.01$). The genetic correlations, however, were more variable; those between FEC and fleece weight were all unfavourable in sign. Two estimates were significant ($P < 0.05$).

In the FEC lines, litter size had a heritability of 0.09 ± 0.02, a repeatability of 0.15 ± 0.01, and phenotypic and genetic correlation estimates with transformed lamb FEC, close to zero. The genetic correlation between transformed FEC and dag score was unfavourable (-0.12) and significant ($P < 0.01$).

In lambs sampled in the autumn, heritability estimates for serum Ig-Tc concentration were 0.08 ± 0.08 in early autumn and 0.29 ± 0.08 in late autumn with an average of 0.18 ± 0.06. The genetic correlation of transformed FEC with Ig-Tc (Table 1) was negative and favourable at -0.47 ± 0.15 overall. Similarly, IgG_1, IgE and IgE-Aspin were all heritable traits and favourably correlated with transformed FEC (see Shaw *et al.*, 1999, 2003). CarLA IgA antibody concentration in saliva was also heritable. Values from log_eIgA data at two sample times from 12 flocks were 0.22 ± 0.05 and 0.31 ± 0.07 with an average of 0.25 ± 0.04. The genetic correlation between the log-transformed values of FEC and CarLA IgA was negative and favourable at -0.49 ± 0.07 overall, with a phenotypic correlation closer to zero of -0.10 ± 0.03 that was still significant.

For the resilience trait, defined as age at first drench, there was a favourable phenotypic correlation with transformed FEC1 of -0.10 ± 0.02 ($P < 0.01$), but the genetic correlation was very close to zero at -0.003 ± 0.084.

DISCUSSION

Heritabilities of egg counts

Estimates of heritabilities of egg counts for lamb FEC, lamb NEM and ewe FEC, were 0.25 or higher, with the exception of NEM1. Estimates of this size were generally consistent with those from other experimental studies in New Zealand, although somewhat higher than for FEC data from industry flocks with heritabilities of from 0.11 to 0.21 able to be derived from McEwan *et al.* (1997) data.

There was good evidence under research conditions that FEC was repeatable from one sampling time to another, with repeatabilities of >0.4 for lamb or ewe FEC, and 0.24 for lamb NEM. Genetic correlations among these egg counts were high at 0.7 to 0.85, when the data were treated as if they were different traits.

Parasite species involved

The worm species present in live lambs of the selection lines were determined each year. In Morris *et al*., 2000 they were summarised as follows: "In all years, lambs were subjected to a wide range of economically important species, including *Haemonchus*, *Ostertagia* [*Teladorsagia*], *Cooperia*, *Nematodirus*, *Trichostrongylus*, *Oesophagostomum*, *Chabertia* and *Trichuris*. In most years, however, *Trichostrongylus* (particularly *T. colubriformis* and *T. vitrinus*) and *Teladorsagia circumcincta* were numerically by far the most important (see Bisset *et al*. (1996)). *H. contortus* was common in some years on a sporadic basis." An examination of the post-mortem burden of worms, and their composition, carried by infected lambs from the two Wallaceville FEC selection lines (Bisset *et al*., 1996) has shown that the live-animal differences, as expressed by FEC, in each of two years of study were mirrored in the differences in worm count post-mortem. Correlations in the first- and second-year lamb crops between FEC and total trichostrongyle burden were 0.91 and 0.85, respectively. The authors also showed that "significantly fewer worms of most of the important abomasal and small intestinal nematode species which infest lambs in New Zealand ….. had established in the low-FEC genotypes than in their high-FEC counterparts." Thus selection for or against FEC had changed the host's resistance to all common nematode parasite species.

Correlations of lamb FEC with live weight, liveweight gain and fleece weight

Phenotypic correlations of weights or gains with FEC tended to be negative, which is favourable, whilst genetic correlations tended to be unfavourable or close to zero, with the exception of that between FEC and weaning weight. The unfavourable genetic parameters reflect the fact that it costs the host nutrients, especially protein (Poppi *et al*., 1986) to reduce the degree of nematode infection in the gastro-intestinal tract (Bisset *et al*., 2001), leaving less protein available for other functions. There are also changes to the properties of the gastrointestinal wall due to inflammation, leading to "leakage" in both directions (Poppi *et al*., 1986). The net result is particularly important in the present Romney data for the unfavourable effect on fleece weight both in yearlings and in ewes with a combined estimate of 0.11 ± 0.03 ($P < 0.01$). Similar findings were obtained from five other experimental studies in New Zealand. These were the Perendale FEC-selection lines (Morris *et al*., 2005), the Coopworth lines at Lincoln University (C.M. Logan, Personal communication), and three sets of fleece weight-selected versus control lines of Romneys; two sets at AgResearch (Morris *et al*., 1996) and one set at Massey University (Williamson *et al*., 1995). However, it is important to note two things about these sheep lines. Firstly, where selection for host resistance was applied, it was expected that lower-FEC sheep would perform better because of lower pasture larval contamination (Bisset *et al*., 1997). Our experimental flock was a mixture of High- and Low-FEC animals. Secondly, it is feasible to apply a selection index in ram-breeding flocks (McEwan et al., 1995), to select for greater production and lower FEC at the same time, as is being done in WormFEC™-recording flocks, because the genetic correlations between FEC and production traits tend to be small in size.

In Australia with Merinos, Eady *et al*. (1998) reported unfavourable genetic correlations of FEC with greasy fleece weight that averaged about 0.15. However, genetic correlations of FEC with live weight at various ages were negative and favourable, with values of -0.20 ± 0.08 at weaning, -0.18 ± 0.09 at 10 months of age, and -0.26 ± 0.12 at 16 months. The nematode challenges in that study included large contributions from *Haemonchus contortus*.

It is not known whether the Romney FEC selection lines differed in intake. Firstly, if they did, as a result of differences in feed required to maintain autumn live weight with Low-FEC minus Control lines differing by 9% in 7-month weight (Wheeler *et al.*, 2008), this would have only amounted to intake differences of ~8 to 10%. Any resulting faecal-egg dilution would have been negligible compared with the 6- to 13-fold difference in FEC between Low-FEC and Control lines at the end of the experiment. Secondly, a feature of the immunological response evoked in the Low-FEC lines, as observed in other studies, was the anorexia (Poppi *et al*., 1990; Kyriazakis *et al*., 1998) which tends to be associated with parasitism in lambs.

Litter size

The genetic correlation between FEC and litter size was non-significant. It is concluded from such small estimates that any realised responses in litter size to direct selection for FEC would also be nil, or very small. Nevertheless, a small favourable correlated response to FEC selection was observed in the Romney lines (Morris *et al*., 2000), with litter size being significantly greater in the Low- than in the High-FEC lines ($P < 0.01$).

Dag score

The genetic correlation of FEC with dag score was significant and slightly negative and therefore unfavourable. This finding was reported originally over two decades ago (Watson *et al.*, 1986). It was a surprise at the time, but is consistent with observations that the resistant host experiences a more acute inflammatory response to a nematode challenge (Bisset *et al*., 1991, 2001). Fluid loss via the gastrointestinal tract due to inflammatory

immune response may be greater in Low-FEC animals, leading to diarrhoea and increased breech soiling. The genetic correlations with dag score may be different under management systems where *Haemonchus* predominates.

Index selection may be used to break the small genetic correlation of -0.12 between FEC and dag score. The present industry recording option in ram-breeding flocks using WormFEC™ services provides a method to achieve this.

Antibody concentrations

Studies of parasite specific antibody responses have led to a better understanding of the immune events leading to improved protective immunity to nematode parasites in sheep (Douch *et al*., 1995, Shaw *et al*., 2003). In general, antibody responses were negatively correlated with FEC. Interestingly, serum IgE-Aspin responses showed favourable correlations with FEC in the selection lines (Shaw *et al*., 2003), but this was not replicated in commercial flocks (R.J. Shaw, Unpublished data). Positive correlations were found between $\log_e$-antibody concentrations (Ig-Tc, IgG_1, IgE) and dag score. This was most evident with early-season antibody responses. Studies of serum IgE responses to Aspin (Shaw *et al*., 2003) and CarLA IgA in saliva (R.J. Shaw, Unpublished data) have identified positive but non-significant genetic correlations with dag score. Genetic correlations between antibody traits and live weights were generally negative or unfavourable, although this was not seen with CarLA IgA. A test using serum Ig-Tc antibodies to nematode larval antigens in sheep was marketed by a veterinary supply company for several years as a means for breeders to select animals with improved immunity to parasites. On theoretical grounds, CarLA IgA offers a further improvement over systemic antibody response (Ig-Tc) as it measures a mucosal antibody response known to prevent larval establishment in sheep (Harrison *et al.*, 2003, 2008). The CarLA saliva test offers easier sampling than blood, better assay standardisation using a purified antigen compared with a crude antigen preparation, higher heritabilities of 0.25 ± 0.04 versus 0.18 ± 0.06, and a similar genetic correlation with FEC overall. CarLA IgA could parallel or augment the existing WormFEC™ service as a method of ranking animals for susceptibility to nematode parasites.

Resilience

From measurements of resilience and FEC in these Romney FEC selection lines, and measurements of resilience and FEC in AgResearch's Romney resilience selection lines, an overall estimate for the genetic correlation between the two traits was close to zero (C.A. Morris, Unpublished data). This is consistent with estimates of essentially zero obtained from industry flocks by Bisset *et al.* (1994) and by Morris *et al.* (2004b).

CONCLUSIONS

FEC in sheep is a heritable and repeatable trait. Selection for low FEC in lambs may lead genetically to slight reductions in post-weaning growth rate, and in ewe and lamb fleece weights. The post-weaning growth rate reductions observed in low-FEC lambs are probably related to a tendency for such lambs to mount a much stronger anti-parasite immune response, as indicated by increased globule leucocyte, mast cell and eosinophil activity in intestinal mucosa, elevated anti-parasite Ig (IgG, M and E) in the blood, and elevated IgA in the saliva. In some individuals this can lead to an increase in dag score. In practice, however, ram breeders should be able to counteract this tendency by using index selection procedures to identify animals showing simultaneously low FEC, low dag score and high production. However, this may slow the rate of progress with FEC. Furthermore, the performance of low-FEC animals can be expected to benefit indirectly from their lower rate of pasture larval contamination. It should be noted that these results may not necessarily apply to other breeds or other countries and management systems.

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