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Effect of selection for productive traits on internal parasite resistance in sheep

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ABSTRACT

Host resistance to internal parasites, as measured by faecal egg count and dagginess was investigated in ram lambs born in the 1981-83 years (approximately generation 3) from the Woodlands selection lines. Lines were selected for either: number of lambs born, 100 day weight, hogget fleece weight and a production index in which all three traits are combined; a fifth line was a randomly selected control. Ram lambs were drenched with anthelmintic and then exposed to contaminated pasture for a period of 6-7 weeks and then faecal sampled. Total plasma protein, albumin and pepsinogen were measured.

The results demonstrated significant variation between selection lines in faecal egg count, dag score, liveweight gain, wool growth and blood plasma parameters. Between selection lines, faecal egg count was positively correlated with liveweight gain (0.95) and wool growth (0.41). Blood pepsinogen and total blood protein were both negatively associated with faecal egg count and liveweight gain (correlations of -0.51 to -0.90).

Using sire variation within selection line (progeny of 65 sires), produced heritability estimates of 0.13 ± 0.07 and 0.25 ± 0.09 for *strongyle* and *Nematodirus* faecal egg count respectively. Significant positive genetic correlations between strongyle faecal egg count and hogget fleece weight were observed.

Keywords Sheep, genetic correlation, gastrointestinal parasites, selection, wool, liveweight.

INTRODUCTION

Young sheep are susceptible to gastrointestinal parasite infection and, if untreated, this results in decreased wool production, reduced carcass weight in slaughtered stock and an increase in mortality rate. Reduction of 30 percent in both liveweight and fleece production are common (Thompson *et al.*, 1982). Recent estimates of the economic cost of internal parasitism in New Zealand sheep suggest direct costs of control and lost production total more than \$260 million per year and this would be increased more than 3 fold if no effective anthelmintic was available (Brunsdon, 1988). Anthelmintic resistance has been documented for all chemical classes in New Zealand and the frequency of anthelmintic resistance on farms has increased markedly during the last decade.

Most sheep develop a moderate to strong resistance to gastrointestinal parasite infection by one year of age. Thereafter sheep are susceptible to heavy infections only if their immune system is compromised by factors such as nutritional stress (including trace element deficiencies) or pregnancy and lactation.

Early development of resistance to gastrointestinal parasites, using faecal egg counts in young lambs as a resistance marker, has been shown to be moderately heritable, whether given an oral challenge (Albers *et al.*, 1987; Windon *et al.*, 1984; Woolaston 1990) or exposed to natural field challenge (Watson *et al.*, 1986; Baker *et al.*, 1990; Bisset *et al.*, 1992). Selection on faecal egg count under defined challenge conditions might offer a prospect of decreased production losses from gastrointestinal parasites in young stock and be an alternative control strategy to anthelmintic usage. However, little is known about correlated changes in other productive traits such as fecundity, growth rate and wool produc-

tion resulting from such selection procedures. Reliable estimates of these genotypic and phenotypic relationships are needed before gastrointestinal parasite resistance can be efficiently incorporated as a breeding objective for dual purpose breeds. Derivation of these estimates is complicated by their interaction with the environment. Environments may range from heavy larval challenges in circumstances where established infections are untreated, to low challenge associated with high frequency of anthelmintic treatment.

In the present study, the correlated change in gastrointestinal parasite resistance to selection for a variety of productive traits were examined in animals grazed in both challenged and unchallenged environments. Half-sib heritability estimates were also obtained and compared with the realised changes.

METHOD

A long term breeding experiment is being conducted with Romney sheep at Woodlands Research Station in Southland. The origin and design of the experiment has been described previously (Tait, 1983). Briefly the trial consists of 5 self-contained selection lines, with 5 two-tooth rams single-sire mated annually within each line. The lines were closed in 1973 and originated from a common base flock comprising over 60 sources of the New Zealand Romney breed.

The selection lines were for number of lambs born per ewe (Dam NLB), 100 day live weight, hogget fleece weight, a production index comprising components of the above 3 traits and a randomly selected control. Animals from all selection lines were grazed together, in appropriate management mobs, except at mating, when mating groups of ewes were grazed separately but

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at a similar level of nutrition. All surviving progeny were retained for evaluation.

Gastrointestinal parasite resistance and related traits were measured on the 1981-83 ram lamb progeny using a field challenge. These animals represent approximately the third generation since selection commenced. At weaning (early December) the lambs were weighed, drenched with 1.5 times the recommended dose rate of levamisole and crutched. They were then left undrenched until faecal egg count approached an arithmetic average of 700-1000 eggs per gram (epg). This required around 7 weeks on pasture that had carried ewes and lambs prior to weaning. When the appropriate epg level was achieved, animals were faecal sampled, dag-scored on a 4 point scale (0, clean to 3, very dirty), scored for faecal consistency (score: 1, pellets to 4, liquid) and blood sampled. Plasma samples were assayed for pepsinogen (high levels indicate abomasal damage), total protein and albumin (low level in both indicate damage to the digestive tract). For progeny born in 1982 and 1983, all 5 selection lines were sampled, but only 3 lines (control, Dam NLB and 100 day weight) were sampled for lambs born in 1981. Clean wool growth over the challenge period was also measured by a modification of the mid-side patch technique (Hawker and Thompson, 1987).

In contrast, ewe lambs were drenched at weaning, again 3 weeks later and then at monthly intervals until June. During the winter period they were grazed on a brassica crop. Liveweights at regular intervals, dag score in July, and hogget fleece weight (February-September, less belly fleece) were recorded.

The data set involved 891 ram lambs and 1,117 ewe lambs, the progeny of 65 sires. Ram lamb data were analysed by fitting models with both fixed and random effects (Harvey, 1977). The final model included measurement year, selection lines nested within year, sires nested within line and year, birth/rearing rank, and age of dam, with birth day as a covariate. Sire variation within year and selection line was used as the error term to compare selection line differences. Before analysis faecal egg

counts (FEC) were transformed ($\log_e(\text{FEC}+1)$ or square root) to normalise the error structure. Comparison of differences between selected lines and the random control provided estimates of realised correlated responses under challenge conditions after selection in an unchallenged environment. The stability of the response across selection lines was determined using simple correlation between selection line means. Paternal half-sib variation within selection lines produced estimates of heritabilities and phenotypic and genetic correlations. The latter method may reduce heritability estimates due to non-random selection within most selection lines. Two environments were involved with the ewe lambs subjected to markedly lower levels of established nematode infection. Thus, for selected traits genetic correlations were also estimated between sex-environment groups using the BI-REML option of Meyer's program (Meyer, 1991). However, these values are subject to the assumption that there were no significant sex by environment interactions.

RESULTS

There was no significant effect of birth/rearing rank or dam age on faecal egg count or faecal consistency score. Lamb age significantly affected faecal consistency score and strongyle egg count with older lambs having drier faeces and lower faecal egg count. The results (Table 1) show significant variation between selection lines in faecal egg count, dag score, liveweight gain, wool growth and blood parameters. The line selected for weaning weight had the highest liveweight gain over the trial period, the highest dag score and the highest faecal egg count. At the other extreme, the random-bred control had the lowest liveweight gain, below average dag score, lowest wool growth and the lowest faecal egg count. Calculation of realised genetic correlation between faecal egg count from selected lines and control produced estimates of 0.32 with hogget fleece weight and in excess of 1.0 for 100 day weight. Differences between individual selection lines and the control could be a result of random genetic

TABLE 1 Least square selection line mean estimates for productive, parasitological and blood parameters¹

	Selection line					
	Control	Index	Dam NLB	100 day weight	Hogget Fleece	Average SEM
Number of animals	202	147	223	193	126	
Dag score	0.86	1.20	0.75	1.25	0.83	0.11***
Faecal consistency score	2.73	2.89	2.63	2.86	2.80	0.09*
$\log_e(\text{faecal egg per gram}+1)$ back transformed means in brackets						
Strongyle	5.73(307)	6.05(423)	6.01(406)	6.28(533)	6.10(445)	0.12***
<i>Nematodirus</i>	0.56(0.75)	0.73(4.6)	0.48(0.62)	0.56(0.75)	0.48(0.62)	0.16NS
Total	5.77(320)	6.11(449)	6.04(419)	6.35(572)	6.14(463)	0.12***
Liveweight (kg)						
20 Jan	26.2	28.7	27.2	29.4	28.5	0.45***
Growth during challenge (5 Dec-20 Jan)						
Liveweight gain (kg)	6.51	6.92	6.68	7.32	7.06	0.23**
Wool growth (g/d)	7.04	7.47	7.11	7.33	8.13	0.19***
Plasma components 20 Jan						
Albumin (mg/ml)	33.3	32.0	32.8	33.1	33.6	0.4**
Total protein (mg/ml)	69.0	67.5	67.0	66.1	67.8	0.5***
Pepsinogen (IU/ml)	0.96	0.71	0.93	0.84	0.68	0.05***

¹ Data are for males only and are adjusted for year, birth/rearing rank, age of dam with birth day fitted as a covariate. Sires within selection line was used as the error term to compare selection line differences.

drift in addition to a response to selection, thus error estimates for the realised correlations are likely to be high and undetermined. Therefore, simple correlations were derived between traits, using the mean of the selection lines, to provide an indication of the consistency of the responses.

Between lines, the total faecal egg count was positively correlated with liveweight gain (0.95), dag score (0.61), faecal consistency score (0.54) and wool growth (0.41). Faecal consistency and dag scores were also positively correlated (0.86). Albumin level among selection lines was not associated with either faecal count or liveweight gain, but plasma pepsinogen and total plasma protein concentration were both negatively associated with faecal egg count and liveweight gain (-0.51 to -0.90). More than 90 percent of the faecal eggs were from *strongyle* worms (*Ostertugia* and *Trichostrongylus* spp.).

Differences in liveweight and hogget fleece weight in ewe lambs, which were regularly drenched, mirrored those recorded in ram lambs.

An alternative method of assessing genetic variation is to use half-sib variation within selection lines (Table 2). The calculated heritability of strongyle count was 0.13 ± 0.07 , with that for *Nematodirus* higher at 0.25 ± 0.09 , and for total egg count 0.14 ± 0.07 . The heritability for dag score was low (0.06 ± 0.06) while that for faecal consistency score was higher (0.27 ± 0.09). All liveweight and wool production traits had moderate estimates of heritability while those for plasma traits were very high. Dag score had significant positive phenotypic and genetic correlations with faecal consistency score (i.e. more liquid faeces with more dags), but had a negative relationship with faecal egg count, although this was not significant. Dag score was also measured on ewe lambs at 10 months of age and was slightly more heritable (0.12 ± 0.06) in this sex, but again had a negative genetic correla-

tion with faecal egg count (-0.73 ± 0.35). Phenotypic correlation of dag score with the faecal egg count was low and positive.

A significant positive genetic correlation was observed between *strongyle* and *Nematodirus* faecal egg count suggesting that lambs susceptible to one genus of nematode tend to be susceptible to other genera. There was no evidence that any animals with high dag scores, faecal consistency scores or faecal egg counts performed more poorly and there is some evidence for the opposite association, particularly with wool production, where a significant positive genetic correlation of 0.80 was observed between strongyle egg counts and wool production over the trial period. A similar significant positive genetic correlation existed between male total faecal egg count and female hogget fleece weight (0.50 ± 0.25). While blood parameters were highly heritable, no phenotypic or genetic correlations were observed with faecal egg count, liveweight gain or wool growth, indicating these traits are of little value in detecting resistant sheep at the moderate levels of infection present in this study.

DISCUSSION

The heritability estimates obtained from this study were lower than previous estimates of heritability of faecal egg counts from a field challenge (Watson *et al.*, 1986; Bisset *et al.*, 1992) except for the estimate for *Nematodirus* which was similar to Watson *et al.*, (1986). These lower estimates could be due to the level and composition of infection or sex effects. The heritability of dag score estimates is similarly lower than previous reports (Meyer *et al.*, 1983; Watson *et al.*, 1986; Bisset *et al.*, 1992). The relationship between dagginess and parasite resistance seems equivocal. In this experiment, the relationship between selection

TABLE 2 Estimates of heritabilities (diagonal), phenotypic (above diagonal) and genotypic (below diagonal) relationships among productive, parasitological and blood plasma parameters¹

Trait	1	2	3	4	5	6	7	8	9	10	11
1 Dag Score	0.06 (0.06)	0.46	0.10	0.02	0.10	0.03	-0.13	-0.07	-0.06	-0.03	0.04
2 Faecal consistency score	1.37*	0.27 (0.09)	0.21	0.09	0.21	0.05	-0.02	-0.03	-0.04	0.01	0.03
3 Strongyle	-0.67	0.14	0.13 (0.07)	0.14	0.99	-0.01	-0.04	0.01	-0.04	-0.08	0.05
4 Nematodirus	-0.27	0.32	0.76*	0.25 (0.09)	0.20	0.06	0.08	0.02	0.01	0.01	-0.01
5 Total eggs	-0.55	0.23	0.99*	0.87*	0.14 (0.07)	0.0	-0.03	0.02	-0.04	-0.08	0.04
6 Wt. 20 Jan	-0.12	-0.04	0.42	-0.40	0.31	0.38 (0.10)	0.63	0.62	0.20	-0.11	-0.08
7 Wt. Gain	-0.08	0.00	0.11	-0.42	0.01	0.91*	0.39 (0.11)	0.41	0.24	-0.07	-0.05
8 Wool growth	-0.03	0.05	0.80*	-0.05	0.72	0.12	0.44	0.18 (0.08)	0.28	0.03	-0.09
9 Albumin	0.44	0.25	0.0	-0.08	0.01	-0.02	0.05	-0.52*	0.37 (0.10)	0.16	-0.03
10 Total protein	-0.32	-0.25	-0.04	-0.16	-0.06	-0.04	-0.22	-0.60*	0.19	0.72 (0.13)	0.05
11 Pepsinogen	0.62	0.30	-0.41	-0.31	-0.39	0.26	0.03	-0.16	0.34	0.13	0.85 (0.14)
mean	0.98	2.8	23	1.2	24	28.0	6.9	7.4	33.0	67.5	0.82
sp	1.01	0.77	10	3.2	10	4.9	2.2	1.8	3.9	4.1	0.46

¹ Half sib estimates from male lambs derived from a model including years, selection lines nested within years sires nested within lines and years, birth rearing rank, age of dam with birthday as a covariate. Traits are as described in table 1 except faecal egg counts were square root transformed. Genetic correlations (* = $P < 0.05$). Standard errors of heritability estimate are listed below the estimate.

lines was positive, but half-sib genetic correlation estimates were negative. Watson *et al.*, (1986) found little relationship on a between strain basis but did obtain a high negative value, similar to this study, from half-sib analysis. Bisset *et al.*, (1992) found a significant positive estimate. Because of the inconsistent nature of the results observed in this study and other studies we cannot recommend use of dag score as a marker for parasitism.

The strong negative relationship observed between parasite resistance (i.e. the inverse of faecal egg counts) and liveweight gain and wool growth in comparisons between selection lines were unexpected. Previous experiments (Albers *et al.*, 1987; Woolaston, 1990; Baker *et al.*, 1990; Bisset *et al.*, 1992) observed that selection for low faecal egg count would lead to little or no change in liveweight or wool production and possibly even favorable responses. Albers *et al.*, (1987) also explored the genetic relationship between these traits, when production was measured in an environment where gastrointestinal parasites were controlled, or under parasite challenge. Their results suggest that parasitic infection results in a favourable relationship between faecal egg count and liveweight gain and wool growth, but that little relationship exists in an unchallenged environment. This contrasts with our results, particularly for wool growth, which were positive and consistent across environments and with both between-selection line and half-sib estimates giving similar results. However, cattle experiments (Mackinnon 1990) suggest that liveweight gain and parasite resistance were negatively correlated genetically, but the relationship depends on the resistance of the genotype examined and the environment to which it is exposed. Our data while persuasive are inconclusive, because genetic drift and sampling problems mean that each selection line is best considered as a single replicate. Thus, evaluation of independent selection experiments should be undertaken as a matter of priority. This has recently been undertaken for the Massey high fleece weight flocks (Howse *et al.*, 1992) and the results are similar to those presented here.

The need for alternative methods of gastrointestinal parasite control other than with anthelmintics is essential and at present, genetic selection appears the most promising. Resolution of whether there are unfavorable relationships between faecal egg count and productive traits, and under what conditions they may exist, is one of the most important aspects facing New Zealand sheep genetic research. Thorough knowledge of the genetic and immunological mechanisms of the relationship could suggest methods by which both production and parasite resistance might be improved expeditiously.

In conclusion, half sib estimates suggest that resistance to gastrointestinal parasite infection is moderately heritable in young Romney sheep in Southland. The high genetic correlation between *strongyle* and *Nematodirus* resistance is encouraging, and suggests that common genetic mechanisms for resistance are involved. However, the strong negative genetic correlation between gastrointestinal parasite resistance and fleece weight is of concern. This relationship was detected between sires within selection lines and also when examining differences between selection lines. In addition, the relationship was consistent whether wool growth was measured either under moderate gastrointestinal parasite challenge in males or when anthelmintic treatment was frequent as with females. Given the importance of this genetic correlation in dual purpose sheep in New Zealand, further work is imperative. Measurement of parasite resistance in all experimental lines of sheep where liveweight, fleece production or fecundity have been selected and vice versa, is the immediate priority. Also, the environment in which animals are

selected and evaluated for resistance to disease should also be given careful scrutiny.

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