DIRECT RESPONSES TO SELECTION FOR DIVERGENCE IN Faecal Nematode Egg Count in Young Romney and Perendale Sheep


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SUMMARY
Experiments undertaken in New Zealand to assess the feasibility and implications of breeding sheep for resistance to nematode parasites have resulted in three different sets of divergent selection lines, each with significant differences in faecal nematode egg count (FEC) following natural challenge. The first involved Romneys established at Wallaceville in 1979, the second Romneys established at Ruakura in 1985 and 1986 (integrated in 1993 with those at Wallaceville), and the third Perendales established at Ruakura in 1986. Overall, divergences in the two most recent lamb crops of the respective High and Low FEC lines were 1.80, 0.65 and 1.19 log units. Expressed in terms of back-transformed values, each High line was passing 7.3, 2.0 and 4.5 times as many eggs as the respective Low line. For the Wallaceville lines, where responses are currently the greatest, the divergence in average breeding value of sires used in 1996 is 2.61 log units, which suggests that further divergence can be expected. In all three flocks, cumulative responses to selection were smaller in the High than in the Low FEC lines relative to the Controls, possibly as a result of constraints to performance imposed by high infection levels in the most extreme susceptible genotypes. The lines are currently providing a valuable experimental resource for studies of the immunological and genetic basis of resistance to gastrointestinal parasite infection in ruminants.

Keywords: Sheep, internal parasites, selection, faecal egg count, response.

INTRODUCTION
Three different sets of divergent selection lines have been set up in New Zealand in recent years to assess the feasibility and implications of breeding sheep for resistance to nematode parasite infection and to provide an animal resource to study the immunological and genetic basis of host resistance. Similar selection lines were established in Australia, and have mainly involved Merinos selected on the basis of faecal nematode egg counts (FEC) following single species artificial challenge (e.g. Woolaston and Piper 1996). In contrast the New Zealand selection lines have involved Romneys or Perendales selected on FEC following exposure to continuous, natural mixed species challenge on pasture. FEC in 4- to 7-month lambs under these conditions has proved to be moderately heritable (Morris et al. 1995), and considerable divergence has been achieved between High and Low FEC lines. Although initially it was believed that resistance to infection would lead to improved productivity under challenge since lambs that suffer the greatest worm burdens would suffer the greatest production losses (Piper and Barger 1988), it is now known that this does not necessarily follow (Bisset and Morris 1996). Nevertheless, two sets of
the New Zealand selection lines are still being maintained as an experimental resource. The purpose of this paper is to summarise the responses to selection achieved to date.

MATERIALS AND METHODS
All three sets of FEC selection lines involved in the present study were located on farms owned by AgResearch (formerly the Ministry of Agriculture & Fisheries). Their histories are as follows: 1. Romneys established in 1979 at Wallaceville Animal Research Centre near Wellington, and selected each year for High or Low FEC in 4- to 7-month lambs following exposure to natural challenge (mainly Ostertagia circumcincta and Trichostrongylus colubriformis) on pasture (Bisset et al. 1996). 2. Romneys established by Ruakura staff in 1985 (Baker et al. 1990), run on two local sites (Rotomahana and Tokanui) until 1992 inclusive, where they were selected as lambs for High or Low FEC as at Wallaceville but with an unselected Control flock also maintained from 1986. From 1993 the elite High and Low animals and all Controls were transferred and integrated with the Wallaceville lines. 3. Perendales established by Ruakura staff in 1986 (Watson et al. 1992), run at four North Island sites until the present day, and selected for High or Low FEC of 4- to 7-month lambs. Artificial challenge was used to generate the test infection (Haemonchus contortus or Trichostrongylus colubriformis) in early years, but subsequently natural challenge was used as at Wallaceville. In all experiments, faecal samples for FEC1 and FEC2 were taken in January (4 months of age) and 6 to 10 weeks later in March/April respectively. In all cases the sampling occasions were separated by a drench, and thus each FEC represented a separate infection. In some production years High and Low line animals were managed on separate farmlets, in order to assess the epidemiological consequences of low FEC selection on lamb productivity, and the contemporary group codes allowed for this situation. All other production years involved selection lines run together. Individual breeding values were calculated using univariate animal-model restricted maximum likelihood (REML) analyses (Johnson and Thompson, 1995), and selection line x year means were obtained from the solution files to determine rates of genetic progress. The two Romney data sets were analysed together as one, taking account of the reference sire links between them. Multivariate models and repeated-record models were also analysed using the same REML programme.

RESULTS
Table 1 shows the divergence achieved over the duration of each experiment. Decisions on ram replacements (numbers of new rams, repeated rams, influence of secondary objectives) have varied over time, depending on finance, and on improving access to timely breeding value estimates for potential young sires and older sires. Flock sizes also varied according to other trial demands.

In the Wallaceville experiment, there was already a wide divergence by year 4, although based on small numbers of animals. Numbers were then increased by a factor of 3 without recourse to artificial insemination or embryo transplanting, and this resulted in substantially reduced divergence. However, divergence had increased again to 1.85 units by year 17 (1995). The Ruakura Romneys were maintained for 8 years and achieved a response of 0.86 units before selected animals were merged with the Wallaceville Romneys in 1993. In the Perendales a
divergence of 1.15 units was achieved in 10 years. In each flock, cumulative responses were smaller in the High than Low lines, relative to the Controls (Table 1).

Table 1. Divergence in breeding values\(^A\) for \(\log_e (\text{FEC}+100)\) between High and Low lines

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Response time (years)</th>
<th>Last 2 yr</th>
<th>(High minus Control)(^E)</th>
<th>(Control minus Low)(^E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wallaceville Romneys</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>0.97</td>
<td>0.46</td>
<td>0.65</td>
<td>1.39(^C)</td>
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<td></td>
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<td></td>
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<td>1.85</td>
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<td>1.80</td>
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<td></td>
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<td></td>
<td></td>
<td>0.68</td>
</tr>
<tr>
<td>Ruakura Romneys</td>
<td>0.57</td>
<td>0.86(^C)</td>
<td></td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.84</td>
</tr>
<tr>
<td>Ruakura Perendales</td>
<td>0.49</td>
<td>1.14</td>
<td>1.15</td>
<td>1.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<td>0.60(^D)</td>
</tr>
</tbody>
</table>

\(^A\) FEC = faecal egg counts, in eggs/g; s.e. of difference between lines = 0.08 \(\log_e\) units
\(^B\) Indicates degree of symmetry of response in the most recent year; complete symmetry = 1.0
\(^C\) Last year before the flocks were merged
\(^D\) Year 9 data, the last for the Control flock

Experimental work with Romney tester-ewe flocks at Wallaceville and Tokanui (Morris et al. 1993), progeny testing selection-line rams over unselected ewes, demonstrated that sires ranked similarly for \(\log_e (\text{FEC}+100)\) at both locations. This testing also provided the Sire Reference links required to combine data from both Romney selection experiments.

Multivariate animal-model REML estimates of heritability for transformed values of FEC1 and FEC2 were 0.23\(\pm\)0.05 and 0.32\(\pm\)0.05 respectively at Wallaceville, 0.25\(\pm\)0.05 and 0.43\(\pm\)0.05 for the Ruakura Romneys (if analysed separately from Wallaceville), and 0.33\(\pm\)0.05 and 0.22\(\pm\)0.04 for the Perendales. Genetic correlations between FEC samples at the two times were 0.94\(\pm\)0.06, 0.53\(\pm\)0.10 and 0.99\(\pm\)0.05 respectively, for the three experiments. If the transformed FEC1 and FEC2 values were treated as repeated records of the same trait, the single-record heritabilities were 0.34\(\pm\)0.04, 0.25\(\pm\)0.04 and 0.26\(\pm\)0.04, and repeatabilities were 0.46\(\pm\)0.02, 0.33\(\pm\)0.02 and 0.54\(\pm\)0.02, respectively.

DISCUSSION

The three experiments described show that it is possible to achieve similar levels of divergence for FEC, using selection based on mixed species natural parasitic challenge, as those achieved in Australian selection studies with single species artificial infection (Woolaston and Eady 1995; Woolaston and Piper 1996). Some of the extra divergence between the High and Low lines after merging the Wallaceville and Ruakura Romneys may have resulted from hybrid vigour, but matings were not specifically set up in 1993 to test this. As shown in Table 1, cumulative responses to selection in all three experiments were smaller in the High FEC than in the Low FEC lines, relative to the Controls. This was a result of constraints to reproductive performance imposed by high infection levels, in rams and ewes with the most extreme susceptible genotypes. Lower net reproduction led to lower selection intensity.
Linear trends for selection response in these three studies are not particularly meaningful, because of changing flock sizes, secondary selection objectives and other factors. Use of selection-line progeny in related sub-trials also compromised opportunities to maximise selection intensity. Divergence between High and Low lines in the most recent two lamb crops (Table 1) led to each High Line carrying 7.3, 2.0 and 4.5 times as many eggs in the three experiments respectively as its Low line. In the longest-running trial (Wallaceville), the average breeding values of sires used in 1996 diverged by 2.61 log units between High and Low lines, which was much more than the ewes to which they were mated. Thus, further responses in FEC can be expected unless there is a loss in genetic variation.

Two of these sets of divergent selection lines are now providing an excellent animal resource for research into the genetic and immunological bases of nematode infection, and various such studies are already underway with these animals.

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REFERENCES