RESPONSE TO DIVERGENT SELECTION FOR OVULATION RATE IN FINN SHEEP

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INTRODUCTION
The Finnish Landrace is one of the most prolific sheep breeds known, reflecting a high ovulation rate, and has been used throughout the world as a source of genetic material to increase prolificacy of local populations (Maijala, 1996). However, the impact of Finn ancestry on production traits other than prolificacy was often unfavourable with consequent lack of producer interest in Finn-cross sheep. Evidence that the heritability of ovulation rate in Finn Sheep is moderate to high (0.5 ; Hanrahan, 1980 ; 1985) suggested the possibility that rapid progress could be made in selecting for increased ovulation rate and hence that a smaller proportion of Finn ancestry would suffice when using Finn genes to enhance prolificacy of target populations (Land, 1978). The evidence for substantial genetic variation in ovulation rate also indicated an opportunity to develop divergent lines which could be an effective tool for the study of the physiological mechanisms determining variation in ovulation rate.

The foregoing considerations led to the establishment of a selection programme on ovulation rate in a closed flock of Finn sheep using intense selection enabled by super-ovulation and embryo transfer to generate the first generation of high and low selection lines (Hanrahan and Quirke, 1982). This paper presents the subsequent response to selection on ovulation rate and changes in liveweight.

MATERIAL AND METHODS
Three lines of sheep were developed during the period 1977 to 1979 as described by Hanrahan and Quirke (1982) using intense selection on ovulation rate (OR) followed by super-ovulation to establish the first generation of a High and a Low line. Following the phase of generating the first progeny generation subsequent reproduction was by natural means and selection was based on the sum of 2 OR measurements (consecutive cycles) at around 18 months of age; from 1985 selection was based on OR measured at around 10 months of age. Males were chosen on the OR record of their dams and were generally used once only as ram lambs. Six sires were used in each selection line and 10 were used in the Control line, with each sire replaced by a son to minimise inbreeding.

Ovulation rate was measured by mid-ventral laparoscopy during the breeding season. In the case of 18-month old ewes the measurement protocol involved initial synchronisation, using progestogen pessaries only, followed by laparoscopy at about day 10 following pessary removal (OR1) and a second laparoscopy 17 days later (OR2). Ewe lambs were not synchronised but were examined in late November and then at appropriate times during December until two independent records of ovulation rate (OR1, OR2) were obtained. The measurement of OR at 10 months of age was initiated with the cohort born in 1981 but only at...
one cycle until the 1984-born cohort when the system of two measurements was introduced. The last cohort of animals in this selection experiment was born in 1997. Selection was temporarily suspended in the late 1980s to allow crossbred matings involving Texel rams, with resulting progeny produced in 1987 and 1988. Selection was on phenotypic performance until 1991 after which an individual animal model was employed to estimate breeding values. All animals were retained until the 18-month measurements were obtained after which unselected females were culled and first lambing was at 2 years of age throughout. The data used in this paper were ovulation and live-weight measurements at 10- and 18-months of age for ewes born between 1993 and 1997. However, OR data for ewe lambs born between 1981 and 1997 are presented to indicate the overall trends.

**Statistical analysis.** Data on ovulation rate and body weight were analysed using Proc GLM of SAS (SAS, 1996). The intra-year repeatability of OR was estimated separately for 10- and 18-month old records.

**RESULTS AND DISCUSSION**
The phenotypic trends for ovulation rate at 10 months of age, based on the average values for OR1 and OR2, are presented in figure 1 for each line. It is evident that the selection has been effective in generating a large divergence between the High and Low lines. It is also clear that there is substantial asymmetry in the response. The line means for ovulation rate at 10- and 18-months for animals born in the 1993 to 1997 period are presented in table 1 along with live weight at the mating. The two components (divergence and asymmetry) of the line differences were both highly significant; almost 80% of the divergence between High and Low lines was due to the increase in the High line relative to the Control line.

![Figure 1. Phenotypic trends for ovulation rate (OR) at 10-months of age in Finn lines selected for Low or High ovulation rate and in the unselected Control (vertical bar = A s.e.)](image)

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Table 1. Least squares means (± s.e.) for ovulation rate and liveweight (ewes born 1992 to 1997)

<table>
<thead>
<tr>
<th>Line</th>
<th>No. of Ewes</th>
<th>Ovulation rate at 10-months</th>
<th>18-months</th>
<th>Liveweight (kg) at 10-months</th>
<th>18-months</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>63</td>
<td>1.61 ± 0.052</td>
<td>2.06 ± 0.058</td>
<td>29.1 ± 0.66</td>
<td>39.1 ± 0.71</td>
</tr>
<tr>
<td>Control</td>
<td>67</td>
<td>2.05 ± 0.050</td>
<td>2.63 ± 0.054</td>
<td>30.6 ± 0.62</td>
<td>42.2 ± 0.67</td>
</tr>
<tr>
<td>High</td>
<td>100</td>
<td>3.70 ± 0.041</td>
<td>4.58 ± 0.049</td>
<td>29.8 ± 0.51</td>
<td>40.3 ± 0.55</td>
</tr>
</tbody>
</table>

F-test for:
- Divergence: P < 0.001 for 10-months, P < 0.001 for 18-months, P > 0.3, P = 0.17
- Asymmetry: P < 0.001 for 10-months, P < 0.001 for 18-months, P = 0.12, P < 0.01

Information on the distribution of OR in each line at 10- and 18-months is shown in figures 2 and 3. The three lines are clearly different at each age and it is evident that the response in the High line was not associated with the emergence of individuals with very high ovulation rate values – as would be expected if selection had acted on a gene with a large effect. The patterns also suggest that the difficulty in achieving response to selection for low ovulation rate is to some extent a scale effect due to the fact that ovulation rate, by definition, cannot be less than unity.

The repeatability of OR at 10-months of age was 0.38, based on estimates calculated on a within-line basis and the corresponding value at 18-months of age was 0.46. Repeatability did not vary with selection line. These estimates are substantially lower than the result from adult ewes (0.66; Hanrahan, 1985). This indicates that heritability of ovulation rate in these age groups is of the order of 0.3 rather than around the value of 0.5 based on data from adult ewes. The CV for ovulation rate varied among the lines; the values obtained were 0.37, 0.24 and 0.25 at 10 months and 0.28, 0.27 and 0.16 at 18 months for Low, Control and High lines, respectively. These results, and especially the low values for 18-month-old High line ewes, reflect to some degree the increased number of ovulation rate classes in the High line. This would be expected to reduce the impact of the discrete nature of the variable on the variation and is consistent with the reducing threshold interval for successive increases in the number of eggs shed. The reduction in relative variability in the High line and the absence of any increase in ewes with very high ovulation rate supports the
hypothesis that genes with a large effect on ovulation are not responsible for variation in ovulation rate in Finn sheep.

The changes in live weight associated with selection appear inconsistent in terms of any genetic correlation with OR. However the High line progeny would have experienced a greater maternal handicap due to high litter size. The lower live weight in Low compared to the Control suggests that the genetic correlation is positive.

CONCLUSIONS
The large divergence in ovulation rate between the High and Low lines (High = 2.2 H Low) confirms the initial conclusions that heritability of ovulation rate was reasonably high in Finn sheep. The response in the High line relative to the Control, was ~ 1.75 times at both 10- and 18-months. Thus, it is projected that a similar proportionate increase occurred at older ages and consequently adult ewes from the High line should have a mean ovulation rate of between 5.5 and 6.0. It is also concluded that the response was not attributable to selection for a gene with a large effect.

REFERENCES