The use of physiological traits in genetic selection for litter size in sheep

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Summary. The objective was to quantify and compare the genetic responses by direct selection on litter size, by indirect selection through a physiological trait and by combined selection, combining litter size and the physiological trait in a selection index. Three kinds of physiological trait were considered, male sex-limited (e.g. testes size), female sex-limited (ovulation rate) and traits measurable in both sexes (gonadotrophin levels).

The results are presented graphically and cover a wide range of possible situations and show the size of the responses for different parameters of the physiological trait. There is usually scope for improvement in the rate of response with combined selection, and also in special cases (high heritability and genetic correlation) with indirect selection. The increases in predicted response may range from zero to two or three times the direct response, depending on the genetic parameters. However, the need for reliable estimates of the genetic parameters is stressed, because the predicted responses might otherwise be overestimated and the selection effort misplaced.

Introduction

Improvement of litter size (lambs born/ewes lambing) in sheep is difficult for several reasons; it is sex-limited to the female, is discrete rather than continuous and has a low heritability (5–10%), although it has a high coefficient of variation (20–40%). Selection within closed lines could, theoretically, lead to annual gains of 0.02 to 0.03 lambs born per year. The results from several selection experiments show rather smaller gains of 0.01 to 0.02 lambs per year compared with unselected contemporary controls (Clarke, 1972; Turner, 1978; Hanrahan & Timon, 1978). Selecting highly prolific ewes out of large populations (Owen, 1976) or from flocks with a selection history (Turner, 1978) have led to new prolific strains, but the development of these strains is not well documented.

It has been argued (Bradford, 1972) that ovulation rate is the main limiting factor to improving reproductive rate in sheep. Land (1974) has proposed the use of physiological traits related to litter size as direct selection criteria. However, the role of such traits in the practical improvement of litter size has not been comprehensively studied so far, and this is the objective of the present work.

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Materials and Methods

Direct selection for litter size (L) is compared with indirect selection for three different kinds of physiological trait, i.e. male sex-limited (M, e.g. testes size), female sex-limited (F, ovulation rate) and traits measurable in both sexes (B, gonadotrophin concentration), and with combined selection, i.e. combining each of these traits with litter size in a selection index. It is assumed that all the physiological traits can be measured before breeding age in the first year of life. To derive the genetic responses from different selection methods, estimates of the genetic parameters are needed. High and low values of the parameters are used to cover a large range of possible sets of parameters so as to allow some general conclusions about the usefulness of physiological traits, and because reliable estimates of the parameters for the traits considered are not available in the literature. The low and high values are 10 and 35% for heritability (with corresponding repeatabilities of 15 and 40%), 0.3 and 0.7 for the genetic correlation with litter size, and with 1 or up to 5 repeated records on the physiological trait.

For rapid genetic response the flock is assumed to be a young one, with males reproducing at 1 year of age and with breeding females in 3-yearly age groups giving an average of 2 litter records per ewe. Litter sizes of 1-1 (70% lambing) and 1-6 (95% lambing) are used for 1-year-old ewes and for adult ewes respectively, with a 10% ewe loss per year. This gives about 37% of 1-year-old ewes in the flock and 124 progeny per 100 ewes. The selection intensity for females is thus 37/62, while a standard 10% selection intensity is used for males, giving a mating ratio of 1/17. The generation interval is 1 year for males and 2-2 years for females, giving a 1-6 year average. In practice there would also be information on contemporary relatives which could be used in selection. The number of paternal half-sibs of each sex is taken as 20, with an average of 10 paternal half-sisters per breeding female, allowing for some selection and loss over time.

The records on paternal half sibs are available currently with an individual’s own records and so they can all be combined in a selection index to assess individual merit. The rate of response to selection for litter size alone (index L) assumes that both male and female offspring are selected on the litter records of their dam and her paternal half-sisters. The indexes for indirect selection for the three types of trait (indexes M, F and B) use the individual and its half-sib family records (one sex only if sex-limited). Finally, litter size information is combined with that for each of three types of physiological trait (indexes (LM), (LF) and (LB)). The indexes can be derived by standard methods from the variances and co-variances among groups of relatives and among traits (Walkley, 1978) and using the program SELIND (Cunningham, 1970). The results are expressed as the estimated genetic response in litter size per year, and take account of the selection differentials and the generation interval for the two sexes and of the accuracy of selection which varies between methods.

While the various figures are chosen to be representative of sheep flocks, they are arbitrary and would vary from flock to flock. However, they apply equally to all the selection methods considered, so the comparisons should not be much affected by the actual figures that apply for any particular flock.

Results

The results are presented graphically in Text-fig. 1. This mode of presentation allows the results for a large number (98) of combinations of parameter sets and selection indices to be scanned and compared. It also shows the effect of variation in the different parameters on the accuracy and response in selection, and allows for interpolation (and some extrapolation) to other parameter values.
Text-fig. 1. Genetic responses from direct selection for litter size (L), from indirect selection through traits which are male sex-limited (M), female sex-limited (F) or measured in both sexes (B), and for combined selection using these indirect traits in selection indices which include litter size. Results are presented for a range of parameter values of the different traits.
The results are given in Text-fig. 1 as the genetic response per year in litter size for a standard deviation of 0-6 lambs in litter size (mean 1-5, coefficient of variation 40%). For the low (and more likely) estimate of heritability of litter size (10%), the response to selection on litter size alone (L) is about 0-03 lambs/year, as other workers have estimated. Greater responses are predicted from indirect selection if the genetic correlation with litter size is high (Examples 5–8 for indexes M, F and B in Text-fig. 1). Moreover, for any particular physiological trait, combined selection (indexes LM, LF and LB) always leads to predicted responses equal to or greater than direct selection because use is made of all the information available. In favourable conditions, responses may be doubled or trebled by indirect or combined selection, so the scope for improvements by related physiological traits is large.

Considering each of the variables in turn, the effect of increasing the number of records (from 1 to 5) for the related traits can be assessed by comparing adjacent pairs in Text-fig. 1 (Examples 1 and 2, 3 and 4, etc.). There are substantial (20–50%) gains in response for indirect selection, especially when the heritability (and repeatability) of an individual measurement is low (Examples 1, 2, 5 and 6). The gains from further records are much less (5–15%) with combined selection because there is already information on litter size. Very similar conclusions apply to changes in heritability of the indirect related traits, with the higher heritability (0-35) giving gains of 30–60% for indirect selection and of 5–10% for combined selection.

The responses depend to a greater extent on the genetic correlation between litter size and physiological trait. This is shown for Examples 1–4 (low) and 5–8 (high) in Text-fig. 1. Increasing the genetic correlation from 0.3 to 0.7 gives increases in response of well over 100% for indirect selection and from 20 to 40% for combined selection. This reflects the fact that the genetic correlation cannot be modified by other means, while the effective heritability (and accuracy of selection) can be increased by taking several records and by adding information on relatives.

The comparative responses for the three types of physiological trait for the same set of parameters are also shown in Text-fig. 1. As expected, responses for traits measured in both sexes (indexes B, LB) were larger than those which were sex-limited to males (by 5–10%) and much larger than those sex-limited to females (15–30%).

Since it uses more information, combined selection is always more effective than indirect selection. The advantage will be greatest when both direct and indirect selection are individually not very effective.

**Discussion**

This work enlarges on previous studies comparing direct selection and indirect selection by considering these, not as alternatives, but as complementing each other in combined selection. The extensions also include use of repeated measurements on the indirect physiological traits and the use of paternal half-sib records which are usually available. By covering a wide range of possible situations in practice it is possible to show the scope for improvement and the size of the parameters required for the physiological traits before they can be useful in selection. The most important parameter is the genetic correlation of the trait with litter size. For low genetic correlations (under 0.3), the gains in response are likely to be small. But as the genetic correlation rises the gains in response can become as large as 50 or 100%. The search in research should therefore be for physiological traits (or combinations of traits) which are intrinsically related to litter size.

As an example of the extra response, suppose that testicular size has a heritability of 30% and a genetic correlation of 0.5 with litter size. It is a trait which is easily measured and simple mass selection could be practised, removing the need for pedigree recording. The gains over direct selection on litter size would be about 15% for indirect selection, and about 50% for
combined selection. Thus if these parameters are appropriate, testicular size could prove a useful tool in improving litter size in sheep. The same conclusions apply to the other types of physiological traits considered, ovulation rate and gonadotrophin concentrations. However, these traits are more difficult to measure and require technical or laboratory tests. Therefore the costs may be higher and the methods may be restricted to breeding institutes or large developmental projects.

**Table 1.** Literature estimates of repeatability and heritability for physiological traits related to litter size

<table>
<thead>
<tr>
<th>Trait</th>
<th>Repeatability (%)</th>
<th>Heritability (%)</th>
<th>Breed</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Testes size</td>
<td>38</td>
<td>40</td>
<td>Finn–Dorset</td>
<td>Land &amp; Lee (1976)</td>
</tr>
<tr>
<td>Ovulation rate</td>
<td></td>
<td></td>
<td></td>
<td>Hulet &amp; Foote (1967)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td></td>
<td>Mixed</td>
<td>Hulet et al. (1979)</td>
</tr>
<tr>
<td></td>
<td>24.69</td>
<td></td>
<td>Targhee</td>
<td>Bindon &amp; Piper (1976)</td>
</tr>
<tr>
<td></td>
<td>89</td>
<td></td>
<td>Merino</td>
<td>Bindon (1975)</td>
</tr>
<tr>
<td></td>
<td>24–67</td>
<td></td>
<td>Merino</td>
<td>Carrick et al. (1976)</td>
</tr>
<tr>
<td></td>
<td>45–68</td>
<td></td>
<td>Merino</td>
<td>Carrick et al. (1976)</td>
</tr>
<tr>
<td></td>
<td>05</td>
<td></td>
<td>Merino</td>
<td>Wheeler &amp; Land (1977)</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td></td>
<td>Blackface</td>
<td>Wheeler &amp; Land (1977)</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td></td>
<td>Finn</td>
<td>Wheeler &amp; Land (1977)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>&lt;00</td>
<td>Galway</td>
<td>Hanrahan (1976)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td></td>
<td>Finn–Galway</td>
<td>Hanrahan (1976)</td>
</tr>
<tr>
<td></td>
<td>66</td>
<td>35</td>
<td>Finn</td>
<td>Hanrahan (1976)</td>
</tr>
<tr>
<td></td>
<td>78</td>
<td></td>
<td>High fertility</td>
<td>Hanrahan (1976)</td>
</tr>
<tr>
<td>Gonadotrophin concentration</td>
<td>−04</td>
<td></td>
<td>Mixed</td>
<td>Hanrahan et al. (1977)</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td></td>
<td>Mixed</td>
<td>Land &amp; Carr (1978)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Merino</td>
<td>Bindon &amp; Chang</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(cited in Bindon &amp; Piper, 1976)</td>
</tr>
</tbody>
</table>

The difficulty in recommending these methods in practice is the lack of reliable parameter estimates for the physiological traits considered. Estimates currently available in the literature are summarized in Table 1. There are few good estimates of heritability, and none of the genetic correlation with litter size. Moreover, estimation of these parameters is not a trivial task, for it will take time and a large number of animals recorded to get reliable genetic parameter estimates. Optimal methods and designs for measuring the parameters are discussed by Hill (1971). Sales & Hill (1976) have highlighted the problem for having unreliable estimates of the genetic parameters. They showed that if an indirect trait is included in an index the extra response predicted will usually be too high if the parameter estimates differ from their true values, and in the extreme case there could be a loss rather than a gain in response. Further caution is also suggested for correlated responses. The prediction of these over several generations is much less reliable than prediction of direct responses (Bohren, Hill & Robertson, 1966) and there may be some consequences of selection on a new physiological trait which are quite unforeseen. On the other hand, because the possible extra responses are substantial, it may be worthwhile to take the risks and start a combined selection programme, using testicular size or ovulation rate, in the chance that the advantages are of the scale indicated.

**References**


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