RECENT DEVELOPMENTS IN WOOL SHEEP BREEDING

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SUMMARY

Recent developments in enhancing the rate of genetic improvement in studs and the capture of this improvement by commercial Merino flocks are reviewed. Despite the lack of information on realised genetic trend, indicators of response including established breeding objectives, measures of selection intensity and accuracy, and the potential for across-flock selection are detailed. Opportunities for enhancing current rates of response include expanded breeding objectives, greater selection efficiency particularly among females, and improving the design and analysis of across-flock evaluation. Many of these enhancements are available and need to be aligned with a more effective process for monitoring expected and achieved rates of genetic progress.

INTRODUCTION

Reviews presented at previous meetings of this and other World Congresses have highlighted developments in breeding objectives and selection criteria for wool sheep (Ponzoni et al 1990, Rogan 1988) and the use of performance recording in Merinos, such as WOOLPLAN in Australia (Brien 1990). The recent World Merino Conference in Uruguay contains overviews of Merino production systems throughout the world and the status of Merino breeding programs (Ponzoni 1994, James 1994). We do not propose to summarise this material here. Rather, we wish to take a broad view of the attainment and capture of genetic improvement within the wool industry as typified by the Australian Merino industry.

The Merino industry has a specialised stud breeding sector with an average breeding ewe flock of more than 700 ewes. Flock rams are purchased by commercial producers, largely from stud flocks, and are the means by which genetic improvement is captured by the commercial sector. This paper poses some fundamental questions on effecting genetic improvement within the industry. For example, is the structure appropriate for encouraging the generation and capture of genetic benefits? What genetic responses are being achieved in the stud and commercial sectors and where are the opportunities for enhancement? Against this background we will also discuss recent and potential developments in wool sheep breeding and its servicing that could have a positive impact on the profitability of wool production.

APPROPRIATION OF GENETIC BENEFITS BY INDUSTRY

Genetic improvement in Merinos relies on within-breed selection by studs with the benefits expressed as increased profitability of wool production in commercial flocks. The principal avenues to achieving effective genetic response in the commercial industry are to increase the rate of genetic progress within stud flocks and/or to enhance the rate of capture of genetic benefits within commercial flocks by promoting a shift of clients towards studs achieving high rates of productivity and away from genetically inferior studs. The impact of increasing genetic gain achieved by studs and increasing the mobility of clients towards higher gain studs have been examined in a model developed by Atkins (1993). Both strategies, separately, led to similar outcomes on total industry benefit but through different pathways. Increasing the proportion of stud breeders achieving high rates of gain had only a modest influence on the market share for ram sales of the high gain breeders but shared the benefits across a wide range of commercial producers, regardless of their mobility. Conversely, increasing the mobility of commercial producers led to a shift in clients from low gain to high gain studs resulting in a marked increase in the market share of high gain studs while the benefits of improved genetic gain were largely captured by clients most likely to change stud source.

In Australia, virtually all our past and current emphasis has been aimed at increasing the rate of progress in stud flocks while the mobility of commercial clients has remained very low, the vast majority of commercial producers never or rarely changing their source of ram purchases. Since the benefits of improved genetic gain are modest and long-term
for stud breeders, in the absence of substantial client mobility, there has been little incentive for individual breeders to adopt higher cost (and possibly higher risk) selection programs. Equally, non-adoption of improved breeding practices would seem to result in relatively small declines in client share for stud breeders achieving low rates of genetic gain. Encouraging a shift of clients towards flocks achieving high rates of gain induces a demand for rams from such superior flocks resulting in a marked increase in market share for these studs. Not only will this demand lead to greater market share for progressive studs, it will lead to obvious incentive for other studs to increase the efficiency of their breeding programs in order to maintain, or at least not lose, substantial sectors of their clientele. In order to maximise genetic response in the Australian wool industry we need to target both rates of genetic response in the stud sector and the capture of this gain by the commercial sector.

GENETIC GAIN IN STUD FLOCKS

Achieved responses in Merino flocks have been poorly documented. The lack of adequate pedigrees has largely precluded genetic trend estimates from mixed model genetic evaluation, such as those estimated by Wilson and Willham (1986) in beef cattle. Time trends in phenotypic production levels have been reported for ram breeding flocks (Rose 1987, Atkins and Semple 1991) but, without estimates of environmental trend, the authors concluded that estimates of genetic responses were uncertain across flocks and inestimable in individual flocks. Analysis of applied selection within a single flock was reported McGuirk et al (1982). James (1987) argued for greater use of planned evaluations, such as the use of stored frozen semen / embryos and the use of control lines, but there have been few developments in this area apart from a control line established by one Australian stud (Hawker et al 1991).

An effective analysis of genetic trend should not only estimate retrospective trend but indicate areas in which greater response could be achieved. In this section we identify the components of gain and the performance of current industry flocks. The information is derived from about 50 flocks which collectively account for 26% and 9% the NSW and Australian stud ewe flock respectively. The components of genetic gain include the definition of a breeding objective, intensity and accuracy of within-flock selection, and use of across-flock genetic variation.

(a) Breeding objectives

The two dominant traits in a breeding objective for Australian Merino sheep remain the weight of wool produced and the fibre diameter of that wool, the latter largely determining spinning performance and end-use. These traits have a moderate to high heritability and a mild genetic antagonism between them. The relative value of a unit change in diameter to a unit change in fleece weight (expressed as a percentage and termed micron premium) is a useful quantification of a breeding objective. The influence of variation in this premium on expected genetic responses in an idealised flock with all selection emphasis on an index of fleece weight and fibre diameter is shown in Fig 1. Genetic responses in the component traits are particularly sensitive to changes in micron premium over a relatively narrow range from 2-3%, where fibre diameter would be maintained at its current level and most improvement achieved through fleece weight, to 10% or more, where most improvement would come from reduced fibre diameter. Personalised breeding objectives have been developed for a number of rambreeding flocks over the past three years, using the OBJECT software described by Atkins et al (1994). The distribution of these objectives for micron premium is also shown in Fig 1. The average objective corresponds with a micron premium of 5.1%, with a range from 2% (fibre diameter maintained and most emphasis on fleece weight) to 8% (major emphasis on reduced fibre diameter and some emphasis on fleece weight).

That most of the personalised objectives lie in a relatively narrow, but genetically sensitive, band of micron premiums might suggest that a single national objective would result in little loss in efficiency. However, the Merino breed supplies a range of wool to service a vast array of end-products, and the breed itself is subdivided in terms of relatively large breeding operations making independent genetic progress possible (Gibson 1992). In addition, the process of establishing a personalised breeding objective has a number of inherent advantages for the subsequent operation of the breeding program:
1. Market values for wool (both absolute price and premium between micron categories) have been subject to wide fluctuation in recent years. For example, micron premiums in the 1993/94 season range from 2% to almost 30%. The variation across years is even greater with annual micron premiums from 2% to 38%. The objective setting process itself cushions or bends the objective within a narrower market range by accounting for genetic consequences. For example, the range of objectives shown in Fig 1 started from a likely market scenario projected by the breeder which averaged 15%, with a range from 3% to 28% micron premium. Choosing a personal objective also diminishes the prospect of consciously or unconsciously altering the objective across years in response to short-term market changes.

2. Examining the effect of alternative indexes on the ranking of potential selection candidates allows the objective to be aligned with the selection process and ensures that independent selection on component traits does not dilute the impact of the index.

3. Breeders have ownership over their personalised objective rather than the group or national objective.

4. Breeders understand the basis of the objective and are then in a position to recognise when it should be modified.

5. The final objective is often set on the basis of a production target(s) over a time period (e.g. a 10% increase in fleece weight or a 1 micrometre reduction in fibre diameter over 10 years etc). This target is translated back to a micron premium appropriate to achieving the target within the constraints of the specific breeding program, or a desired gains index (Brascamp 1984) by iteration.

(b) Within-flock selection

(i) Selection intensity. A useful measure of the potential genetic response can be obtained from the selection intensity that could be applied to male and female replacements entering the breeding flock, and the generation interval of both sexes within the flock. Loss of potential selection intensity can arise through selection decisions made early in
life before records on the economically important traits in the breeding objective are available. In Table 1, the sample of flocks previously recorded for breeding objectives are shown in terms of their potential selection intensity (numbers selected of total numbers available), effective selection intensity (numbers selected of total numbers measured), and generation interval, separately for males and females. Selection intensities among females were both lower and more variable than those among males. Female selection intensity was substantially higher in flocks with an open-nucleus structure of two or more tiers of females, leading to a higher variability among flocks. The loss of selection intensity before measurement was relatively greater in females, and the difference between potential and effective intensities represented a reduction in available numbers of about 20% in both males and females.

Table 1 Measures of selection intensity and accuracy among Merino breeding programs, expressed as mean and coefficient of variation (c.v.)

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
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<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>c.v. (%)</td>
</tr>
<tr>
<td>Selection intensity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(standardised selection differential)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Potential</td>
<td>2.47</td>
<td>7</td>
</tr>
<tr>
<td>Effective</td>
<td>2.32</td>
<td>13</td>
</tr>
<tr>
<td>Generation interval</td>
<td>3.37</td>
<td>19</td>
</tr>
<tr>
<td>Selection accuracy</td>
<td>0.44</td>
<td>18</td>
</tr>
<tr>
<td>aggregate genotype</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Selection emphasis (%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>- predicted</td>
<td>59</td>
<td>18</td>
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<tr>
<td>- retrospective analysis</td>
<td>55</td>
<td>35</td>
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(ii) Correlation between index and objective. The actual selection criteria used for selection will influence the accuracy with which genetic superiority can be identified. Within Merinos, the traits recorded, the age at which they are recorded, the use of adjustments for environmental / maternal effects, and including information from relatives can all influence the correlation between the measured index and the objective. Atkins (1990) reviewed the information on age effects and the potential value of repeat information, concluding that both can contribute to differences in accuracy of selection. The high heritabilities of the dominant traits in the objective result in a high correlation between the index and aggregate genotype. Despite differences in the recording of measured traits and the use of additional information, variation in selection accuracy among males was relatively small across flocks (Table 1). Compared with males, selection accuracy among females was lower.

(iii) Achieved selection emphasis. While fleece weight and fibre diameter are the dominant traits in a breeding objective, other traits are important. For example, body weight, reproduction rate, disease resistance and additional wool quality traits can be of direct economic importance and are often included in a formal breeding objective (Ponzoni 1986). Additionally, there are further traits, such as those related to conformation and protection from the environment, that are visually assessed and account for some of the available selection differential even when they may have no correlation with performance (Lewer and MacLeod 1990). An indirect measure of the impact of these additional traits is to estimate the selection emphasis, defined as the percentage of the total selection differential applied to the measured traits in the index of a nominated objective. Predicted selection emphasis (Table 1) indicated that only 59% of the effective selection intensity available for males was used on index traits and even less among females. That such predictions are realistic is supported by a retrospective analysis of the selection decisions among groups of candidate rams in 27 flocks (Table 1), where the selection emphasis averaged 55% with a spread from less than 20% to more than 90%.
(iv) Selection among adults. Casey and Hygate (1992) surveyed the majority of NSW studs and found that more than 50% of all sires were 3.5 years (third mating opportunity) or older and 20% were at least 5.5 years. The distribution of sire breeding values for homebred sires within age for our data set (Table 2) showed wider variation than anticipated within flocks without selection. Further, correlations between breeding value and number of progeny were essentially zero, indicating little evidence of effective selection of sires across ages.

(d) Across-flock selection

The opportunities for utilising between flock genetic variation have been greatly enhanced by the development of artificial insemination by frozen semen in sheep. In order to fully capture the potential benefits, flocks must be linked to allow animals to be evaluated across locations. The lack of available links for many flocks has led to the development of central test sire evaluations where individual sires from a number of stud flock sources are evaluated by progeny test in regionally based test stations (Roberts et al 1991). The main purpose of this approach is to allow leading stud sires to be evaluated for a wide range of traits under closely monitored conditions so that industry will be assured of the accuracy and fairness of the evaluation. The traits recorded commonly include fleece traits at both 1- and 2-years of age together with body weight, disease resistance indicators and visual traits related to conformation, productivity and wool quality.

For each test station (currently 6 throughout Australia) only 12-16 sires are evaluated each year. The design of sire evaluation for linked analysis was considered by Miraeti Ashtiani and James (1991, 1992). They showed that for such evaluations involving different source flocks, about 30% of total progeny should be by link sires for traits with a heritability of more than 0.3. Since 1989, the proportion of total progeny bred from link sires has averaged 28%. Results from sire evaluation have been combined across years and sites for measured (Cottle et al 1993) and visual traits (Atkins et al 1993). The distribution of central test sire breeding values for fleece weight and fibre diameter are shown in Table 2 for medium-wool sires, fine-wool sires and a combined evaluation that used links from on-stud evaluations since the fine wool site is not formally linked with the medium-wool sites. Relative to the expected and estimated within-flock distribution, central test sires show a much wider spread in performance, indicating the importance of between-flock differences as a source of genetic variation.

Table 2 Standard deviation of breeding values for fleece weight and fibre diameter among sires

<table>
<thead>
<tr>
<th></th>
<th>Fleece weight (%)</th>
<th>Fibre diameter (μm)</th>
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<tr>
<td><strong>Within-flock</strong></td>
<td></td>
<td></td>
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<tr>
<td>expected (no selection)</td>
<td>5.6</td>
<td>0.80</td>
</tr>
<tr>
<td>estimated</td>
<td>6.3</td>
<td>0.87</td>
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<tr>
<td><strong>Central Test</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medium wool</td>
<td>7.5</td>
<td>1.02</td>
</tr>
<tr>
<td>Fine wool</td>
<td>9.0</td>
<td>1.14</td>
</tr>
<tr>
<td>Medium + Fine wool</td>
<td>11.8</td>
<td>1.36</td>
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</table>

A criticism of central test sire evaluation is that available spaces for sires are few compared with the numbers of rams used within studs, although effective prior selection would reduce the imbalance. However, a secondary purpose of central test sire evaluation is to provide a structure and database that allows individual flocks to link to central test either by submitting one or more home-bred rams or by purchasing semen from central test rams to evaluate in the home flock. By establishing such links with central test, the contributing flocks are also linked together allowing comparisons among many more rams. This process will allow a wider set of industry initiatives:

1. Comparison of central test rams with other rams from the same source which allows pre-selection of rams for entry to central test that are likely to be superior based on an initial within-flock progeny test.
2. Progeny test ranking of rams relative to central test rams even though the rams may only have been evaluated within their source flock.

3. Across-flock evaluation using central test links. The links available within industry flocks are so poor that without additional links from central test no across-flock evaluation would be possible for many flocks. The establishment of central test has allowed across-flock evaluation to become a real possibility.

**CAPTURE OF GENETIC GAIN IN COMMERCIAL FLOCKS**

Since the stud sector supplies the vast majority of rams used by commercial producers, genetic gains made in studs are directly transmitted to commercial flocks with a lag in actual production between the stud and its client flocks (Hill 1974). Additionally, the opportunity exists for commercial producers to exploit genetic variation that may exist among stud sources for current performance. Evaluations of teams of commercial wethers have been widely used in Australia since the late 1970's. Teams are entered from commercial flocks with a named stud source. The results from a single comparison are of little value because of the small number of teams and the limited number of animals per team. Atkins et al (1992) showed that combining information across many such comparisons gave relatively precise information on comparative productivity of 53 stud sources (Fig 2). Differences between studs covered the range of -17% to +14% for fleece weight and -11% to +10% for fibre diameter. A very similar range in performance was recently reported by Poggenpoel and van der Merwe (1992) among 40 South African studs linked by sires from a common control line. Variation in profitability of these sources is extremely high under many market scenarios. By identifying the current stud source and a commercial breeding objective, commercial producers are able to identify alternative stud sources that will improve productivity. In choosing an alternative, it is necessary to also consider the likely genetic gain that each stud source will achieve so that an appropriate balance between current and future (current + likely gain) production will be achieved.

![Figure 2 Distribution of genetic differences between studs for fleece weight and fibre diameter estimated from linked wether comparisons (Atkins et al 1992)](image-url)
FUTURE DEVELOPMENTS

With less than 60% of the available emphasis for selection being applied to measured traits in males and significantly less in females, there are deficiencies in both the definition of the objective and the effectiveness of selection. The breeding objective and predictor traits can be expanded to include additional measures of wool quality, disease resistance and food intake. Visual selection is applied to wool quality traits yet most have an objective measure available and an identifiable economic value. Traits such as staple length and fibre diameter variability perhaps need to be included despite their modest economic value so that their influence on selection is not over-emphasised. Staple strength and some components of style require more precise estimates of genetic parameters (Piper 1992). Genetic improvement of disease resistance, particularly resistance to helminths and blowflies, is attractive as a non-chemical control strategy and as a reaction to increasing chemical resistance by the parasites. Desired gain indexes (Woolaston 1994) would seem a sensible option for including disease traits and overcomes the difficulties of attaching an appropriate economic value. Field measurement of pasture intake is now allowing genetic parameters to be estimated (Lee et al 1994) so that feed intake can be included in the objective more appropriately. But, monitoring of index selection is required since a personalised objective does not guarantee a consistent selection emphasis.

Selection among females is one area that appears inefficiently exploited both in terms of selection intensity and accuracy. Not only does this inefficiency limit response in current selection programs, it severely limits the potential of multiple ovulation and embryo transfer (Gaffney et al 1991) which relies on donor females being accurately selected. The lack of effective across-age selection, particularly among sires, was surprising given the wide variation that apparently exists. While sire evaluation currently relies on designed progeny tests, since full pedigrees and effective female records are rare, a move to animal model BLUP would be of significant value in improving adult selection while retaining unbiased evaluation. The collection of full pedigrees in large Merino flocks is a substantial cost, and the availability of cheap DNA fingerprinting could be an attractive alternative (James 1994).

The wide differences between stud flocks create both an opportunity for selection and a difficulty for evaluation. There is a need to form groups for analysis particularly where there is significant regression of breeding values due to limited numbers of progeny. But grouping will also exacerbate the sometimes tenuous links between flocks, years or sites. The continuation of central test sire evaluation to improve connectedness will be a key strategy for some time. The limited number of link rams and the reliance on decentralised measurement laboratories to supply within-flock evaluations are not favourable for a transition to across-flock evaluation. The situation, at least in the short term, is analogous to the combination of breeding values of dairy sires across countries (Goddard 1992). Infrequent (perhaps annual) analysis of a centrally maintained database could be used to produce breeding values for sires. Subsequent within-flock evaluation would then use de-regressed sire information of relevance to the particular flock. A centralised database for Merino sire evaluation has already been established (Swan et al 1992).

With an effective across-flock evaluation scheme in place, it could be argued that commercial product evaluation is no longer required, since between flock differences will be captured by the evaluation scheme. But commercial product evaluation can and does give information on lifetime production and additional wool traits not routinely recorded in within-flock evaluation. In addition, it provides comparative information across a range of production environments. Although genotype X environment interactions are rarely important for production traits (Woolaston 1987), interactions are observed for overall economic performance and secondary traits such as fleece rot and some wool quality factors.

Perhaps the most important conclusion is that we can monitor Merino improvement programs. Even without the benefits of full flock and pedigree recording, we have identified some simple indicators of the performance or 'health' of a breeding program, such as breeding objectives or production targets, efficiency of within-flock selection, sire usage and trend, and across-flock comparisons. With such information available at modest cost, real improvements in rate of genetic progress can be recommended and collaboratively put in place. Coupled with the required information to allow commercial producers to make effective decisions to capture these benefits and thus provide the stud sector with ongoing
incentives, a healthy adoption of genetic technology and commercial benefits would seem assured.

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REFERENCES