RELEVANCE TO PRODUCERS OF RESEARCH INTO THE GENETIC IMPROVEMENT OF REPRODUCTIVE PERFORMANCE

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I. INTRODUCTION

In recent years Animal Production Committee has established several panels and workshops to consider recommended breeding programmes for Australia's major livestock industries. Ensuing reports have listed improved reproductive performance as a major breeding goal, thus implying that selection can increase reproductive performance, to the benefit of the relevant industries. Both of these issues will be considered in this review. The major emphasis will be on improving sheep reproductive performance, mainly because of the considerably greater body of information available on that species, much of it emanating from Australia.

II. WHY IMPROVE REPRODUCTIVE PERFORMANCE?

Improving reproductive performance is likely to increase both the biological and economic efficiency of animal production enterprises (Dickerson 1970). One of the major costs in most production systems is that of maintaining the breeding female. Increasing reproductive performance (the number of offspring produced annually by each breeding female) will spread this fixed cost over a larger number of offspring available for sale (Piper & Bindon 1976). Nevertheless, there may be costs associated with increasing reproductive performance and these have to be considered when assessing the desirability of such a change. Specifically, there may be higher feed costs during gestation and lactation, or increased post-weaning costs per offspring, because of their smaller size at weaning (Dickerson 1970). With dairy cattle and sheep, a higher level of reproductive performance may also have adverse effects on the breeding female's own production.

III. THE IMPROVEMENT OF REPRODUCTIVE PERFORMANCE BY SELECTION

Selection for increased reproductive performance can operate on overall measures of performance, such as the number of offspring produced per breeding female per year. However, the consequences of such programmes are often more readily appreciated by considering the major components of performance and this review will concentrate on two of these, fertility, the ease with which a female conceives, and fecundity, the number of offspring produced per conception (Bindon 1974). No attempt will be made to assess the likely success of selecting for a shorter re-breeding interval or for increased lamb survival for want of relevant published information.

In any selection programme, response depends on the selection pressure applied and on such population parameters as the repeatability and heritability of the trait. One of the difficulties in selecting for increased reproductive performance is that it is a sex-limited characteristic and male breeding values can only be estimated from the

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performance of their female relatives. Work currently in progress suggests that endocrinological or anatomical characteristics of the ram may be indicators of his breeding value for fecundity, and LH levels and testicular growth rates have been specifically mentioned in this context (Land 1974; Bindon & Turner 1974). Nevertheless, the value of such criteria in within-flock selection programmes has still to be demonstrated.

**Fertility**

Selection for increased fertility is likely to yield only limited improvement, primarily because the maximum level of performance is 100% of females conceiving to a specific joining. In addition, the low estimates for the repeatability and heritability of fertility, on average less than 10% (see Turner 1968; Inskeep et al., 1961), indicate that the rate of advance towards this upper limit is likely to be slow. Progress is likely to be even further reduced if the age structure of the population is altered, to enable dry females to be culled (Forrest & Bichard 1974).

**Fecundity**

Recent emphasis on the improvement of reproductive performance has focused on the possibilities of improving fecundity where progress is not limited in the same way as it is for fertility. In addition, fecundity has generally been found to be more highly heritable in sheep (Purser 1965; Forrest & Bichard 1974), of the order of 10%, while similar estimates have been obtained in pigs (Strang & King 1965). The heritability of fecundity is usually higher at birth than at later ages (see Turner 1968), and so selection is normally seen as operating on litter size at birth, with management practices being adjusted to ensure that a high proportion of those born are weaned.

The heritability of twinning in cattle has previously been considered to be so low as to offer little hope for improvement. More recently it has been appreciated (Johansson, Lindhe & Pirchner 1974; Piper & Bindon 1976) that heritability estimates obtained using untransformed data markedly underestimate expected progress in a selection programme, as indicated by the difference in twinning between daughters of single and twin-producing cows (Johansson, Lindhe & Pirchner 1974). Nevertheless, with the low incidence of twinning in cattle, selection differentials in a within-herd selection programme for increased fecundity would be small, and expected progress very slow.

**Response to selection**

A number of Merino flocks have been selected for increased reproductive performance in Australia. Several of these are maintained by CSIRO (Turner 1968), although the Booroola flock had been subjected to commercial selection for increased reproductive performance for 10-15 years before CSIRO acquired part of it in 1959. Their other flock selected for increased reproductive performance, the high-twinning flock T, was established in 1953. In both of these flocks, selection of replacement rams and ewes has been on the basis of their dam’s reproductive performance. To do this, ewes with differing numbers of lambing records must be compared and tables have been developed (see Turner 1968) which facilitate this procedure.

While a full description of selection procedure and responses in the Booroola and T flocks will be published shortly (Turner, in preparation), a guide to litter sizes currently being obtained is given in Table 1.
The performance of the low-twinning flock (0) is similar to that obtained in the unselected control flock at Armidale, so that the differences observed between T and 0 provide a reliable measure of the response to selection for increased twinning.

TABLE 1
Lambing performance in Merino flocks selected for increased reproductive performance

<table>
<thead>
<tr>
<th>Flocks</th>
<th>Percentage of ewes giving birth to the following numbers of lambs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>CSIRO Armidale</td>
<td></td>
</tr>
<tr>
<td>High twinning flock (T)</td>
<td>15.8</td>
</tr>
<tr>
<td>Low twinning flock (0)</td>
<td>11.0</td>
</tr>
<tr>
<td>Booroooola flock</td>
<td>8.3</td>
</tr>
<tr>
<td>Trangie</td>
<td></td>
</tr>
<tr>
<td>Fertility flock</td>
<td>14.0</td>
</tr>
<tr>
<td>Control flock</td>
<td>18.9</td>
</tr>
</tbody>
</table>

Average performance, 1970-1972, ewes 2-7 years of age
Average performance, 1972-1974, ewes 2-6 years of age

Selection for increased reproductive performance is the major breeding goal in the Fertility Flock at Trangie (Dun & Eastoe 1970). The flock was started in 1959 and twin-born ram and ewe hogget replacements, are chosen in preference to singles. Any ewe failing to rear a lamb is culled, regardless of age or previous performance. This selection programme has increased litter size by 2% per year, and has also reduced the incidence of dry ewes (Table 1, Atkins & McGuirk, unpublished data).

IV. THE CONSEQUENCES OF INCREASING REPRODUCTIVE PERFORMANCE BY SELECTION

If selection can increase reproductive performance, what might the more general consequences be? For example, how will increasing fecundity (the most likely avenue of making worthwhile improvements in reproductive performance) affect:

(1) the number, value and cost of production of animals reared to marketable age, or
(2) the productivity (milk or wool) of the breeding female.

It is unlikely that any changes in other aspects of production will come about as a result of a genetic antagonism between these traits and reproductive performance. In general, estimates of such genetic correlations are low in both sheep and pigs (Turner 1972; Morris 1975). There may be a negative correlation between fleece weight and lambs born per ewe joined (Turner 1972; Barlow 1974), but the available information is conflicting.

There is considerable evidence that increasing reproductive performance will reduce the performance of individual breeding females and their offspring as a direct environmental effect on performance. In general, information on these 'environmental effects' has come from the relative
performance of animals falling into different reproductive states (for example, dry, single-bearing, twin-bearing etc.) or being born in litters of different size. In the majority of such studies the animals themselves decided their own experimental levels, and so these 'environmental effects' may have some small genetic component.

Effects on the young

As litter size increases so survival of the young declines. Numerous comparisons have been made of the relative survival of the single and twin-born lambs (see Turner 1968), and some information is available on single and twin-born calves (Hendy & Bowman 1970). While death rates are higher among the twin-born, the twin-bearing female still weans a considerably higher number of young (Turner 1968). This result can be seen clearly in the Fertility Flock at Trangie where the majority of lambs are born as twins. Litter size has been increased at birth (1.32 v 1.10, Table 1), and by only a slightly lower amount at weaning (1.12 v 0.95, Atkins & McGuirk, unpublished information) using a drift lambing system in which some triplet lambs are fostered (Giles 1968). In fact, nearly all of this improvement in lambs weaned is retained when no assistance at all is given at lambing (Tyrrell & Giles 1974).

Results such as these cannot be extrapolated to cover larger litters. In the Booroola flock (Table 1), triplet-bearing ewes wean more lambs than twin-bearing ewes if the lambs are artificially reared indoors (Turner & Neumann, in preparation). However, under field conditions at Armidale, many triplet and higher-birth order lambs appear to be too light to survive, even when they are given continued assistance to stand and suckle during the first 24 hours after birth (L.R. Piper, personal communication). Similarly with pigs, there is evidence that for specific management systems, there is a litter size beyond which the total number of piglets weaned per sow declines (Glastonbury 1976). Again, alternative management strategies, particularly the use of early weaning methods, may enhance survival from large litters.

There is considerable evidence that as litter size increases, so growth is adversely affected up to (Pattie 1965) and even after weaning (Standal 1973). As regards wool production, the adverse effects of being born a twin generally persist until hogget shearing (Turner 1961; Drinan 1968).

In cattle one additional feature associated with twinning is that approximately 90% of all female calves born in heterosexual twin-pairs are freemartins (Marcum 1974), over 20% of all twins born. However, the number of fertile females available for selection is not reduced in a twinning herd and as freemartins are easily identified and have unimpaired growth rates, they may legitimately be regarded as a bonus; additional animals available for slaughter.

Effects on the breeding female

The breeding female has a higher feed requirement than one which is not pregnant (Weston & Hogan 1973), and marginal feed requirements increase with litter size (Large 1970). The importance of these increases will differ between species and production systems, depending on feed costs during these critical periods. With sheep and beef cattle, late pregnancy/lactation often coincides with periods of maximum pasture production, so that increasing reproductive performance may simply reduce feed wastage.
As reproductive performance increases, so wool production declines (Mullaney et al., 1969; Rose 1974), and both pregnancy and lactation contribute to this effect. In dairy cattle the available evidence suggests that twin-bearing cows tend to be higher than average milk producers, even in the lactation initiated by the birth of twins. Yields may be lower in the lactation during which the cow bears twin foetuses (Wood 1975).

Based almost entirely on dairy breed data, twin-bearing cows tend to suffer from an increased incidence of retained placentae and calving difficulties, and to have an increased rebreeding interval (Hendy and Bowman 1970). These are possibly the major reasons why culling rates have been found to be higher among twin-bearing cows in both Europe and North America (Johansson, Lindhe and Pichner 1974; Wood 1975). It should be emphasised that these problems exist for twin-bearing cows in herds in which most cows are producing one calf, and where the level of management is presumably geared to the single-bearing cow. The magnitude of these problems may be reduced by improved nutrition in the latter part of pregnancy (see Hendy & Bowman 1970), hence the need for a reliable method for the early detection of cows carrying twin foetuses.

V. RELEVANCE OF RESEARCH FINDINGS TO PRODUCERS

A guide to the present relevance of any research finding to producers might well be the extent to which they adopt practices recommended as a result of that finding. With breeding programmes, and specifically selection programmes for increased reproductive performance, adoption would mean that producers:

(1) accept that increased reproductive performance is a major breeding goal, and

(2) have available to them and use the means of achieving improvement in reproductive performance.

While the assessment of producers' attitudes to breeding goals is a speculative and highly subjective business, there does appear to be general acceptance of the importance of a high level of flock or herd fertility to overall profitability. This view is strongly felt among pig and dairy producers, where the cost of maintaining an unproductive female are high. These two forms of production are also intensive and so offer the greatest scope for identifying and culling females of low fertility.

While the possibilities for increasing fecundity are much more encouraging, producers would seem to be less enthusiastic about increasing litter size than they are about ensuring that all females produce young. This attitude would appear to be most widespread among Merino breeders and dairy cattle producers while in the past, the question of increasing twinning in beef cattle perhaps has not received serious consideration at all. On the other hand, if the figures reported by Fogarty, McGuirk & Nicholls (1976) were representative of the performance of British breeds of sheep in Australia, then it may well be more important to concentrate on improving fertility. The general lack of acceptance of increased fecundity as a breeding goal for sheep and cattle could well be that producers recognise the production costs to the individual animal of say producing twins or being born a twin, and are not so immediately aware of the possible benefits of increased fecundity to the biological and economic efficiency of their herd or flock.

As a breeding goal, increased reproductive performance has to be
considered along with the other selection options open to the producer. While a high level of reproductive performance may be necessary for efficient and profitable production, greater economic benefits may be obtained by selecting for other characters. By selecting for increased reproductive performance we reduce the selection pressure which can be applied to other characters, and this reduction can be important if we restrict sire selection in cattle and sheep populations to say among the twin-born.

To operate an effective selection programme for increased fecundity, it is necessary to identify animals of superior genetic merit. Here the major difficulties are likely to be encountered with sheep selection programmes, mainly because of the numbers of animals involved and the extensive conditions under which most flocks are run. Efficient and cheap methods of identifying twin-bearing ewes and twin-born lambs have been listed as major areas for research for some considerable time but currently available procedures for identifying twins are generally not acceptable to producers. If the industry was convinced of the value of twins, the acceptability of their existing procedures might automatically be increased.

When discussing breeding programmes it is important to appreciate that their success is dependent upon implementation in those herds or flocks which supply males to the industry (Richard 1971; McGuirk 1976). Commercial producers who by males can do little to influence long-term genetic improvement of their stock. Indeed, in the Merino, any short-term genetic improvement which individual producers might make as a result of ewe selection programmes could well operate in the face of selection against twinning in many studs. Replacement breeding stock in the studs are generally selected at an age when twins are at a disadvantage, and unless twins are identified and their performance adjusted appropriately, single-born animals are likely to be preferentially selected.

In cattle, while it may be relatively easy to identify the twin-born calf, the low incidence of twinning would render any within-herd selection programme ineffective (Piper & Bindon 1976). For worthwhile improvements it would be necessary to select superior stock across herds and from as large a population as possible. This is the approach adopted by the CSIRO in establishing their high-twinning herd, where particular attention is given to choosing animals with a history of repeated twinning (Piper & Bindon 1976).

Enhancing the acceptance of increased reproductive performance as a breeding goal.

What might be done to achieve greater acceptance of increased reproductive performance, especially increased fecundity, as a breeding goal? Or, given that there are likely to be both advantages and disadvantages, how might producers be encouraged to make perhaps a better-informed assessment of the overall consequences of increasing reproductive performance by selection?

One approach would be to attempt to justify recommended breeding programmes to producers on economic grounds, using available information on the relative productivity of females of differing reproductive performance, and of their progeny. Clearly more comparative data of this sort is required, even for the Merino, and it should be available for a wide
range of environments. The critical need is for a thorough economic
evaluation of such data.

With Merino producers a more effective way of challenging current
industry attitudes to increased fecundity would be to foster an expanded
commercial evaluation of rams from the experimental flocks listed in
Table 1. Robertson (1974) has already indicated the extent to which
lambing percentages in commercial flocks can be increased in this way.
More extensive evaluation of such genetic material, on commercial pro-

caperties, would enable producers to assess the long-term effects of se-

lecting for increased fecundity under commercial conditions and to expe-

cIENCE the problems likely to be encountered. In future years, the high-
twinning herd established by CSIRO could well serve a similar role. Such
evaluation may lead to greater direct exploitation of these experimental
populations.

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