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have fallen below that necessary for a large response (Martin *et al.*, 1979).

These results demonstrate that an annual booster is necessary to improve reproductive performance since unboosted and untreated 2-tooths had similar levels of performance but lower than that of boosted 2-tooths. This probably resulted from inadequate antibody titre levels in unboosted ewes.

The limited data on 4-tooth ewes suggest that a higher level of reproductive performance was achieved in ewes immunised as hoggets. An increased response following treatment of ewes in successive years has been reported (Cox *et al.*, 1982). In addition, there is some suggestion that a booster can be delayed for 24 months. However, larger numbers of ewes are needed to substantiate these findings. The poor response in ewes first immunised as 4-tooths may have been due to the high level of

performance in untreated control ewes. Smith (1983a) found no ovulation rate response in a group of ewes with a high natural ovulation rate (i.e., 2.16 v 2.19).

In summary, these findings demonstrate that the immune system for oestrone is competent from early age in sheep. A booster is necessary to improve reproductive rate. The immunomemory system for the oestrone-HSA conjugate appears to remain competent for at least 24 months after the last booster vaccination. A hogget immunisation may be associated with an improved response to subsequent annual boosters.

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## Implications of steroid immunisation for programmes of genetic improvement of sheep

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#### ABSTRACT

Immunisation has implications for genetic improvement programmes by influencing the intensity of selection, the amount and nature of genetic variation able to be exploited by selection, the accuracy of the selection process or by adding flexibility to animal husbandry that might otherwise be the objective of dynamic crossbreeding strategies.

Since immunisation changes the reproductive rate of a flock there are consequential effects on the intensity of selection that is possible. Improving the effective lambing percentage from 120% to 140% can increase the intensity of selection of female replacements by about 19%. The improvement is less on the male side, the combined effect on genetic improvement in a ram-breeding flock of 400 ewes being about 6%.

Alteration to the balance of physiological events may even serve to display genetic variation not otherwise available for selection. Good evidence is available that natural ovulation rate is a useful selection criterion for improvement in lamb production, but there is no direct evidence on the value of selection following immunisation of ewes to steroid hormones controlling reproduction.

Indirect evidence for sheep that litter size responses to immunisation are essentially additive with respect to the effects of age of ewe, flushing treatment, breed and strain differences, suggests no major antagonisms with natural ovulation rate. Indirect evidence from mice is not so comforting — Land and Falconer's selection experiment for natural and PMS-induced ovulation rate gave an estimate of only 0.33 for the genetic correlation between these two traits, suggesting that they were largely independent genetically.

Regardless of the true genetic situation for sheep it seems important that recording programmes recognise and adjust for the different distributions of ovulation rate and litter size under natural v immunised circumstances.

**Keywords** Immunisation; selection intensity; genetic parameters; physiological genetics; lambing percentage; performance recording.

#### INTRODUCTION

Altered reproductive physiology leading to increased lamb output per ewe, whatever the cause, has potential implications for programmes of genetic improvement in 3 broad areas. Firstly, it can affect breeding objectives through changes in the relative

emphasis appropriate to different traits or components of the underlying production or profit function (Melton *et al.*, 1979), which it is sought to maximise by selection or crossbreeding. Secondly, it can affect genetic responses to selection: through the intensity of selection, the accuracy of the selection,

the amount and nature of genetic variation able to be exploited by selection or through effects on the timing of the selection process. Thirdly, improved reproduction can assist gene dissemination from ram-breeding to commercial flocks.

The purpose of this review is to discuss these potential implications with respect to changes in lamb production following steroid immunisation.

### DUAL PURPOSE BREEDING OBJECTIVES

Commercial sheep breeders and producers are often less enthusiastic than researchers about the relative importance of reproductive to other traits. They also often tend to be adamant about the lesser importance of lamb to wool production in difficult production environments compared with those more favourable for reproduction. This difference in attitude perhaps stems from changes in the distribution of litter size as the mean lambing performance of the flock rises (McGuirk, 1976). Multiple born animals usually have the dual handicap of lowered meat production and increased costs of production on a per lamb basis. Nevertheless, the economic efficiency of sheep production usually rises as the result of marginal improvements in lambing percentage, especially from a low initial flock mean (Morris *et al.*, 1982; Nitter, 1982).

Reproductive responses to immunisation would seem to offer no new arguments to these principles. From evidence produced in the trials reviewed in accompanying papers there appears to be no major change in the distribution of reproductive performance following immunisation, providing reductions in embryo and post-natal survival are counted along with improvements in ovulation rate.

It is often argued that improvement of reproduction by non-genetic means will allow the emphasis of selection to be moved from a trait with a low heritability (net reproductive rate or lamb production) to traits like wool production and lamb growth whose heritabilities are higher. These arguments ignore other components of the selection process and their costs and benefits in addition to the costs associated with the non genetic technique (e.g., immunisation) itself. In particular, reproductive performance shows high genetic variation and as a consequence, similar percentage rates of economic improvement (of generally higher marginal economic reward) to those associated with lamb growth and wool production.

### SELECTION RESPONSE

A useful description of selection response which shows its separate underlying components is given by the following formula:

$$R = ih \sigma_A / L \text{ (Falconer, 1981)}$$

where R is the annual selection response,

i is the average intensity of selection or standardised selection differential across both sexes,

h is the square root of the heritability, or accuracy of selection in the case of indirect selection using a correlated trait,

$\sigma_A$  is the genetic standard deviation for the trait or profit function in which improvement is sought,

and L is the average generation interval for males and females combined.

The genetic consequences to selection for improved reproduction through immunisation are examined separately for each term in this equation.

### Selection Intensity

Improvement of net (or effective) reproductive rate, measured at the stage at which selection takes place, has an important impact on the intensity of selection. This occurs whatever the cause of the change in the effective lambing percentage. The effect is illustrated in Table 13 taken from a larger table used by Clarke (1982) in his discussion of improvements in reproduction arising from cross-breeding with new prolific breeds.

Improving the effective lambing from 100 to 120% increases the intensity of selection among female replacements by about 19%. The effect is less on the male side, the combined effect on genetic improvement in a ram-breeding flock of 400 ewes being about 6%. However the percentage improvement reduces as the mean effective lambing percentage of the flock increases.

These increases apply regardless of the character which is the focus of genetic improvement through selection.

**TABLE 13** Effect of lambing percentage on selection intensity in units of the phenotypic standard deviation (400 ewe flock).

	Effective lambing percentage			
	80	100	120	140
Male selection intensity (4 best rams saved)	2.34	2.42	2.48	2.55
Female selection intensity (27% of stock replaced)	0.53	0.74	0.88	0.98
Average flock selection intensity	1.44 (100)	1.58 (110)	1.68 (117)	1.77 (123)

### Selection Accuracy

Non-reproductive traits.

The lack of evidence of any major side effects of immunisation on animal performance other than indirectly through changes to the reproductive process suggests that neither the genetic expression of

non reproductive traits nor their genetic associations with one another or with the reproductive traits themselves are likely to be affected. Current methods of adjusting for the effects of litter size on growth and wool production records in performance recording programmes should accordingly continue to be appropriate to enable young animals to be ranked accurately regardless of whether they came from immunised or non immunised dams.

#### Reproductive traits.

In the case of predictions of breeding merit for reproductive traits such as ovulation rate or the number of lambs born completely different arguments apply. Firstly, there is the obvious need to adjust for the higher average reproductive performance of immunised ewes, especially if some lambing records are made following immunisation and others are not. This adjustment could be particularly complicated if a variable immunisation policy were practised from year to year and would need to take account of the carry-over effects of immunisation which, like the immediate effects themselves, seem to vary from year to year and with different types, batches and methods of immunisation. Many performance recording schemes like Sheepplan may cope with this variation to some extent since they deviate records from age and year means before processing these adjusted deviations for prediction of breeding merit for average lifetime performance. Sheepplan in its present form would not, however, cope with a varying policy of immunisation in which only some or different ewes were treated each year. To do this would require some sort of management group coding with which to attempt to adjust for the effects of specific immunisation histories on lifetime reproductive performance.

A second concern about the accuracy of selection for reproductive traits is the extent to which genetic variation is displayed under immunisation and whether the genes being evaluated by performance recording are the same ones as under a non immunisation regime. The first will determine whether genetic improvement of performance under immunisation is possible from selection and the second whether any improvement would carry over to be displayed without immunisation. No direct evidence is available on these questions.

#### Physiological considerations.

In the absence of marked genetic antagonisms among the separate events, the sequential nature of the reproductive process leads us to expect that genetic variation seen at an early stage will contribute in some degree to variation in lamb production (Cockrem, 1979). Alteration to the balance of physiological events may even serve to display genetic variation not otherwise available for selection.

The effect of marked genetic antagonisms has been clearly seen in mice where selection for ovulation rate was balanced by an increase in embryo loss, with the result that litter size remained unchanged (Land and Falconer, 1969). It seems that in mice and pigs (Johnson *et al.*, 1984) genetic variation in embryo survival makes an important contribution to genetic variation in litter size. By contrast in sheep, there is good evidence that natural ovulation rate is a useful indicator of genetic variation in lamb production (Land, 1974; Hanrahan, 1980). Ovulation rate changes certainly seem to be the basis of litter size responses to selection (Hanrahan, 1984; Meyer and Clarke, 1982). Indeed, it has been convincingly argued (Hanrahan, 1982; Hanrahan and Quirke, 1985) that selection for litter size in sheep would be more efficient if ovulation rate rather than litter size itself were used as the criterion of selection, i.e., that underlying genetic variation is better displayed by avoiding the non-genetic masking influences of embryo survival.

Unfortunately as yet there is no direct evidence of the value of selection for either ovulation rate or litter size following immunisation. J.P. Hanrahan (pers. comm.) is in the process of gathering information on the repeatability between years of ovulation rate following immunisation and on the correlation between natural and immunised ovulation rate, which should provide some early leads.

Land *et al.* (1983) postulate that by looking more closely at physiological criteria which control ovulation, the search for indirect measures of breeding merit for reproduction may be taken even further back in the reproductive process than ovulation. They have examined research on the activity of follicle stimulating hormone, luteotrophic hormone, prolactin and on ovarian sensitivities to these hormones from this point of view. The sensitivity of gonadotrophin release to the production of negative feedback hormones from the ovary is a further avenue of study. Immunisation however is but one method whereby this feedback may be manipulated with a view to displaying genetic variation among animals; administration of endogenous hormones is another.

The latter method was studied for mice by Land and Falconer (1969) in an experiment in which selection was practised for natural ovulation rate and for ovulation rate induced by injection of PMS. Both lines responded to selection with realised heritabilities of 0.31 and 0.22 for natural and induced ovulation rates, respectively. However, quite different physiological mechanisms appear to have been responsible in each case. The response to high natural ovulation rate appeared to have been due to changes in FSH activity, whereas changes in induced ovulation rate appeared to result from changes in ovarian sensitivity to gonadotrophin. Thus, quite

different biology was involved. The low realised genetic correlation estimated between natural and induced ovulation rate (+0.33) suggests that the responses were to a large degree genetically independent as well. There were certainly major differences in their genetic association with litter size. Selection for natural ovulation rate gave no increase in litter size, whereas selection for induced ovulation rate increased litter size. Bradford (1969) by contrast found that selection for ovulation rate following gonadotrophin treatment gave no response in litter size.

In line with ovulation rate results for mice, Bodin (1979) found for Lacaune ewe lambs studied as part of a performance recording scheme, that the paternal half-sib estimates of the genetic correlation between natural and PMS-induced litter size was also low (+0.39). The single-record heritability estimates for the 2 traits were 0.03 and 0.06, respectively.

Direct evidence will be needed for sheep if immunisation becomes important in the future. Early leads determining the need for direct experimental investigation of genetic control could come from studies of the repeatability of ewe performance.

Indirect evidence for sheep that litter size responses to immunisation are essentially additive with respect to the effects of age of ewe, nutritional treatment, breed and some strain differences, suggests no major antagonisms with natural ovulation rate at least at the phenotypic level. That responses have been higher for animals carrying the Booroola gene suggests that the physiological mode of action of immunisation on the control of ovulation complemented that of the Booroola gene.

### Generation Interval

In selection programmes the generation interval determines the amount of time before another round of selection can take effect and it is usually measured as the average age of the (selected) parents when their offspring are born. Immunisation is unlikely to have major effects on the generation interval unless there are important management reasons for differential treatment of ewes of different age or unless some aspect of the immunisation response itself can be used to obtain an early estimate of breeding merit for reproductive performance. There seems no sound basis to either of these possibilities at present.

### GENE DISSEMINATION

If indeed immunisation proves not to be useful for early recognition of genetic merit for lamb production, under either natural reproduction or

following immunisation, then gene dissemination programmes which actually serve to lengthen the generation interval may become necessary. One practical possibility could be to base evaluation of breeding merit for reproduction on early natural ovulations or lambings and to use the immunisation technique for improved gene dissemination from selected ewes. For ram breeding flocks whose present breeding programmes are heavily committed to improvement of natural lamb production, the approach has the advantage of avoiding any uncertainty about different genes being concerned in the expression of ovulation in immunised ewes. Specific study of the merits of such a policy has not been made. Such study should also consider endogenous hormone treatment, embryo transfer and artificial insemination as alternative methods of boosting rates of gene dissemination to the commercial sheep industry.

### CROSSBREEDING

Crossbreeding is a major avenue of genetic flexibility for meeting changing production objectives. Ch'ang and Atkins (1982) stress this aspect for sheep production in Australia where crossbreeding occupies a pivotal role in diverting breed resources from the wool to the meat producing sectors of their sheep industry. Immunisation favours this process, the higher reproductive rate allowing greater opportunity for crossbred matings over and above the purebred matings needed for flock replacements.

### SUMMARY

Immunisation offers flexibility to sheep production which can have genetic consequences to selection objectives and crossbreeding practices. Improved reproduction also increases selection intensity. For a 20% lambing rate response to immunisation, the effect on genetic improvement in a ram-breeding flock of 400 ewes is about 6%.

The relative degree of inheritance and whether the same genes are involved in the expression of reproductive rate under natural and immunised lambings is not known. Indirect evidence suggests no genetic antagonisms with major production traits. Repeatability studies are suggested as a prelude to direct experimental investigation of genetic control.

Even if entirely non-genetic, the effects of immunisation on reproduction must be accommodated by recording schemes if advantage is to be taken of improved gene dissemination through better rates of reproduction under immunisation.