CONTRACT REVIEW

REPRODUCTIVE MANAGEMENT OF EWES FOR EXTENSIVE WOOL PRODUCTION

R. J. SCARAMUZZI

CSIRO Division of Animal Production, P.O. Box 239, Blacktown, N.S.W. 2148.

INTRODUCTION

The pre-eminent position of Australia as a producer of fine Merino wool will continue to be based on extensive production of wool under natural conditions.

However, producers of fine wool will face increasing competition from synthetic fibres and alternative natural fibres. Merino wool producers need to respond to this challenge if they wish to remain competitive in the market place. Higher production efficiency, that is a greater output to input ratio, is one way of achieving this. There is a large scope for improving production efficiency through reproduction because under extensive conditions, reproductive rate is low and highly variable (Scaramuzzi 1988). Increasing reproductive rate has many effects that are beneficial to production efficiency but these need to be balanced against some drawbacks.

Reproductive research that identifies suitable genotypes and that provides flexible management options is important to the future of the Merino wool industry. From such research improved reproductive strategies that are simple and cost-effective can be developed. Labour intensive therapeutic intervention and the application of advanced reproductive technologies are unlikely to have a direct major impact on production efficiency. However, indirect genetic gains will accrue more rapidly with the application of reproductive technology. This contract illustrates from recent research how an understanding of reproduction in the Merino can be developed into management practices to enhance reproductive efficiency.

ENVIRONMENTAL LIMITATIONS TO REPRODUCTION

G. B. MARTIN[AB], J. S. FISHER[A] and N. R. ADAMS[B]

*School of Agriculture (Animal Science), University of Western Australia, Nedlands, W.A. 6009.
[B]CSIRO Division of Animal Production, Private Bag, P.O., Wembley, W.A. 6014.

Each breeding season can have one of several outcomes for a ewe; she may or may not reproduce, and, if she does, she may have a single lamb or more than one. Giving birth can be potentially life-threatening to both ewe and lambs because the ewe must survive the metabolic demands of pregnancy and lactation and provide her lamb(s) with the metabolic reserves to survive. Two environmental factors limit survival: (i) food supply (in the Merino wool industry this means supply of pasture); (ii) hypothermia: the greatest danger for the newborn lamb (Donnelly 1984).

Food supply is the dominant influence on survival. The ewe needs to predict the food supply over the period from late pregnancy to the end of lactation. She uses two sources of information: (i) her own body condition from metabolic signals that reflect her reserves of energy, protein and perhaps minerals; (ii) a knowledge of the seasonal cycles obtained primarily from photoperiod that allow her to predict pasture conditions in the future. Photoperiod is the best long term guide to the seasons because other cues, such as temperature or food supply, are modulated by local (i.e., climatic) factors that can vary widely over short periods.

Using photoperiod the ewe can predict the food supply 6 months ahead. In temperate climates (e.g. Tasmania), this works extremely well; the ewe ovulates in autumn, carries her fetus(es) over the period of poor pasture growth and low environmental temperature, then lambs and lactates during the spring and summer when temperatures are higher and pasture is abundant. The lambs are then weaned after a sustained period of maximal growth and can survive the next winter without maternal assistance. This system is ideally-suited to reliable climates where there is an abundance of pasture in summer and autumn.

In contrast, most Australian wool flocks are maintained in mediterranean or pastoral regions. The dominant breed is the Merino, an ‘opportunistic’ breeder, that has developed strategies to cope with an unpredictable climate. Photoperiod sets the pattern for the annual reproductive cycles in the same way as for temperate breeds, this pattern is modulated in three ways: first, the spontaneous (photoperiodically-driven) breeding season begins in mid-summer (Fig. 1), so Merino ewes would generally larnb in mid-winter; second, the Merino ewe can by-pass the photoperiodic control of the breeding season through the 'ram effect' and advance mating to spring or early summer (Martin *et al.* 1986); third, the Merino ewe can rapidly respond to nutritional signals and change her breeding activity, primarily by changing ovulation rate (Stewart and Oldham 1986). This opportunistic breeding strategy is particularly suited to the semi-arid environments of Queensland and NSW.

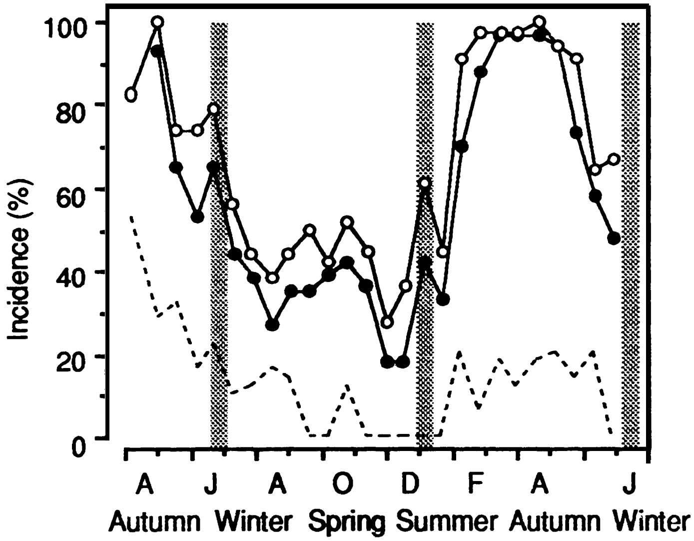

Fig. 1. The annual rhythms of oestrus (●), ovulation (○) and twinning rate (---) for a flock (*n* = 34) of 4-year-old Merino ewes maintained at a liveweight of around 40 kg. The ewes were run continuously with vasectomised rams. The shaded columns represent the winter and summer solstices. Adapted from Oldham *et al.* (1990).

By contrast, in mediterranean climates (e.g., WA and SA), the ewe that relies on a purely photoperiodic mechanism is effectively misinformed about the future because summer-autumn is the period of paucity and spring is the period of abundance.

Nutritional reserves at mating

The breeding season would normally be the season in which the Merino ewe expresses her full potential for multiple ovulation (King 1976). Her body reserves are good, but they are falling and the reproductive system is acutely responsive to her current nutritional status. Faced with the risk of insufficient reserves in late pregnancy and lactation, the ewe has a single ovulation (Fig. 2). This is a major factor limiting reproductive rate in mediterranean-type environments (Knight *et al.* 1975). Under these conditions, the nutritional status at the time of ovulation is a poor guide to the likely availability of feed in 5-6 months time when the nutritional demands of the lamb are maximal. Indeed, it could be argued that no breed of sheep is well suited to a mediterranean environment, where the optimal time of breeding in late summer is a time of substantial feed deficiency. Short-term nutritional supplements (e.g. lupins) can be used to deceive the ewe into expressing her normal twinning rate but, to date, this approach has proven unreliable and is not cost-effective as a management tool (Croker *et al.* 1985).

Nutritional reserves during pregnancy

From mating onwards, the food supply deteriorates, body reserves are low and can become critical during late pregnancy. This problem is serious if winter pasture does not grow in time for lactation, a real risk because the timing of the break of the season varies.

Ambient temperature

An early breeding season means high ambient temperatures, often above 33°C, during the mating period, and reduced fertility (Lindsay *et al.* 1975). Moreover lambs are born in winter when cold, wind and rain will compound the effects of lack of maternal reserves and poor pastures. The survival of twin lambs of Merino ewes can be improved when their mothers are adequately fed (King *et al.* 1990).

The ram-induced breeding season

Very early mating, in spring or early summer, has the ewe at her peak in terms of body reserves and the metabolic signals will favour multiple ovulation. However, the spring-summer photoperiod has a strong inhibitory influence on ovulation rate so spontaneous multiple ovulations are rare. This problem can be overcome by the ram effect itself, but only if the ewe conceives at the first or second ovulation induced by the rams (Oldham *et al.* 1990). Another disadvantage to ram-induced breeding is that lambing will be very early, perhaps in the middle of autumn. Temperatures are conducive to good survival, but feed and the metabolic reserves of the ewe are depleted by the summer-autumn feed shortage. If the break of the season were delayed, the situation would become catastrophic for the ewe and lamb.

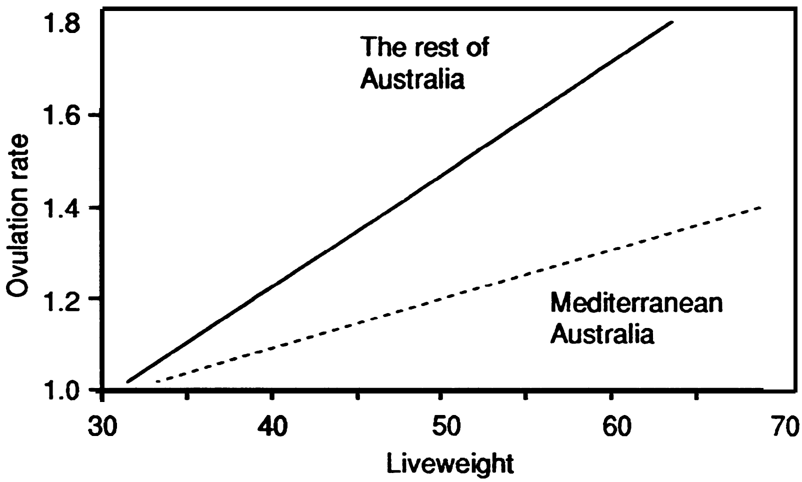

Fig. 2. The relationship between liveweight and ovulation rate in ewes from different parts of Australia. The regression line for mediterranean regions is adapted from Lindsay *et al.* (1975), and that for other regions is adapted from Morley *et al.* (1978). When ewes in mediterranean regions are fed lupin grain, the slope of the regression line increases to match the rest of Australia.

Conclusion

The Merino ewe appears to have the genetic capacity to avoid most of the problems associated with extensive wool production in semi arid or mediterranean climates. The capacity for opportunistic breeding could be adapted to most Australian climatic regions and to extensive (low input) management systems. Under normal circumstances, the farmer can supply extra feed (as pasture) at critical periods so the environmental threats to survival are reduced. However, controlled breeding methods to overcome normal reproductive and survival strategies are not cost effective or fully reliable.

OVERCOMING CONSTRAINTS: THE RAM EFFECT

D. R. LINDSAY, J. F. WILKINS and C. M. OLDHAM

Dept of Animal Science and Production, University of Western Australia, Nedlands, W.A. 6009.

Until recently artificial control of oestrus has been confined to stud animals for artificial insemination and other reproductive manipulation, but has not been used extensively for wool production. Control of reproduction is nonetheless desirable in naturally mating flocks but, in to-day's economic climate, only if it can be achieved at low cost. The use of the 'ram effect' offers a possible

Table 1. Mating and conception in ewes synchronised by the ram effect and joined by natural service with different percentages of rams

Different letters indicate significant differences within rows *(P < 0.05)*

	Percentage of rams in mating group		
	1%	3%	6%
Ewes presented	575	286	286
Ewes marked	357	242	264
Percentage of those presented	62b	85a	92a
Ewes pregnant	268	183	227
Percentage of those presented	47a	64b	79c
Percentage of those marked	75a	76a	86b

solution. The constraints to successful synchrony of oestrus using this technique have been well described by Pearce and Oldham (1984). Briefly, it is a question of having the maximum number of ewes in seasonal anoestrus, having them sensitive to the sudden introduction of males, and avoiding short cycles which upset the synchrony of oestrus. Most Merino sheep in Australia are in anoestrus from September until mid to late January (Oldham *et al.* 1990) although the depth of anoestrus or proportion of spontaneously cycling ewes appear to vary from season to season. Sensitivity to the introduction of males depends on a period of isolation although the circumstances, timing, and degree of this isolation are still to be clearly defined (Pearce and Oldham 1988). Short cycles can be completely eliminated with a single dose of 20 mg progesterone at the time of introduction of rams (Cognie *et al.* 1982).

A further important constraint in natural mating of ewes synchronised by the ram effect is the capacity of rams to mate with large numbers of ewes in oestrus simultaneously. Clearly, the 1% of well-prepared rams proposed by Lindsay *et al.* (1976) would be insufficient but what increase is needed in numbers of rams when mating of the entire flock is reduced to only a few days? We have recently completed a series of experiments aimed at answering this question and examining the feasibility of synchronised natural mating for controlled breeding in sheep.

Mating groups consisted of 2 rams with 200 ewes (1%); 3 rams with 100 ewes (3%); and 6 rams with 100 ewes (6%). These groups were replicated 3 times, involving a total of about 1147 ewes. The rams were chosen for medium serving capacity (Blockey and Wilkins 1984), and for scrotal circumference of 31 cm or greater. The ewes were given a single injection of 20 mg progesterone on 9 November and were run with 12 teaser rams to induce cyclical activity. Fifteen days later the ewes

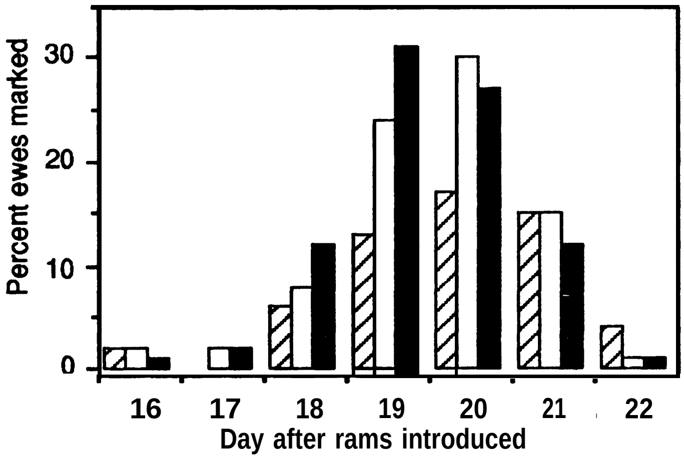

Fig. 3. Distribution of matings for ewes joined with 1 (□), 3 (□) or 6% (■) of rams after synchronisation by the ram effect.

were randomly allocated among the 9 mating groups in separate paddocks of 5 ha. Raddles were used, and ewes were inspected daily between the 16th and 22nd day for raddle marks. Pregnancy was determined using real time ultrasound between 22 and 25 days after mating. Ewes were re-examined about 73 days after mating.

The performance of the ewes is summarised in Table 1, and the distribution of matings in the synchronised cycle is shown in Fig. 3.

The results illustrate that it is possible to achieve satisfactory conception (around 80%) from a synchronised natural mating lasting less than 1 week. To do so requires more rams than is normally accepted. One per cent of rams were unable to mark the ewes presented to them in the 6 days available and, even in the ewes that they mated, conception was significantly lower than with 6% of rams (Table 1). Three per cent of rams were as successful as 6% of rams in marking ewes but, despite this, conception rate in the marked ewes was lower (Table 1).

The ram effect is a cheap and powerful option open to woolgrowers for manipulating reproductive activity in their flocks provided that their ewes are anoestrus and that there are rams in sufficient numbers to mate up to 35% of the flock in a single day. The practical potential of this option makes a compelling case for completing the research to establish a management program that ensures reliable responses over a wide range of conditions.

OVERCOMING CONSTRAINTS: NUTRITION

J. A. DOWNING and R. J. SCARAMUZZI

CSIRO Division of Animal Production, P.O. Box 239, Blacktown, N.S.W. 2148.

In self-replacing Merino flocks the breeding strategy is usually to breed a sufficient number of ewe lambs to allow for the replacement of ewes culled for age and other losses and to enable genetic selection for improvement in desired fleece characteristics. The greater the number of ewes weaned the greater the selection pressure that can be applied. The number of ewes weaned can be increased by either increasing the proportion of breeding ewes in the flock and/or by increasing the lambing rate of individual ewes. The lambing rate of individual ewes is limited, in the first instance, by ovulation rate. Although maximum ovulation rate is determined by genotype, its expression is influenced by a number of non-genetic factors of which nutrition is perhaps the most important.

Nutrition will influence the number of lambs weaned at many points in the sequence of reproductive events between gamete production and weaning. The production of spermatozoa and oocytes, early embryonic survival and neonatal survival are all deleteriously affected by limitation to the nutrient supply at critical times. This paper will concentrate on the relationship between nutrient supply and ovulation rate. Other aspects of the nutritional effects on reproduction have been covered in recent reviews (Lindsay *et al.* 1991).

It is well established that a positive relationship exists between absolute body weight and ovulation rate and between increasing body weight and ovulation rate. These have been defined respectively, as the ‘static’ and ‘dynamic’ effects of nutrition. The latter phenomenon is also referred to as ‘flushing’. In more recent times it has been reported and repeatedly confirmed that acute changes in nutrient supply at critical times will also increase ovulation rate without a measurable change in body weight (eg the so called ‘lupin’ effect). The maximum genetic expression of ovulation rate can been obtained by either keeping breeding ewes at a high body weight or by maintaining them at moderate body weight and then increasing the nutrient supply in the few days before mating. It is possible that the second option is a valuable alternative where feed supply is highly seasonal and the seasonal excess in supply can be stored as feed rather than fat. The mechanistic relationships between nutrient supply and ovulation rate are not well defined and controversy still exists as to the exact nature of this relationship. To become an effective management strategy, the short term effects of nutrient supply on ovulation rate must be reproducible under a wide range of farming conditions.

The feeding of a lupin grain for 4 days at a critical time during the oestrous cycle will increase ovulation rate (Stewart and Oldham 1986). Use has been made of this observation in studying the role that specific nutrients may play in these short term effects. Rumen degradation of dietary protein and the consequent production of microbial protein from rumen digestion of carbohydrate poses major problems in determining the effects of specific nutrients. This problem can be overcome by infusing the nutrients directly into the peripheral circulation or into the abomasum.

Plasma concentrations of gonadotrophins and some metabolic hormones have been measured during the late luteal phase in ewes fed a lupin supplement. The lupin supplementation resulted in an increase in ovulation rate without statistically significant changes in gonadotrophin levels. Plasma concentrations of prolactin and insulin were elevated while those of growth hormone were depressed.

The infusion of glucose for 5 days also increased ovulation rate and this was achieved without an increase in gonadotrophin levels. Prolactin levels were temporarily elevated during the infusion while there was no significant change in the levels of growth hormone. The expected increase in insulin levels was observed.

The effects of specific amino acids were studied by infusing them for a period of 5 days. The infusion of tyrosine, a mixture of tyrosine and phenylalanine, tryptophan and aspartic acid had no significant effect on ovulation rate or plasma hormone levels. However the infusion of a mixture of leucine, isoleucine and valine did increase ovulation rate. This effect was produced without significant change in the plasma levels of growth hormone, prolactin or the gonadotrophin. Insulin levels were significantly elevated in the ewes infused with a mixture of leucine, isoleucine and valine.

These studies led us to consider that insulin and growth hormone might play a role in mediating nutritional effects on ovulation rate. The changes observed in ovulation rate following improved nutrient supply occur while the ewe is undergoing metabolic change mediated by the metabolic hormones. The ovary like all other tissues will be responsive to these changes. If the metabolic hormones play a role in ovulation rate responses our data suggest that they are most likely to do so at the level of the ovary. This may be to either enhance the action of gonadotrophins on follicles or modulate ovarian feedback control of the circulating levels of FSH.

If we are able to understand the way in which nutrition can influence ovulation rate it is likely that we will be able to make better use of available nutrients to increase ovulation rate.

THE INFLUENCE OF REPRODUCTION ON WOOL GROWTH

D. G. MASTERS

CSIRO Division of Animal Production, Private Bag, P.O. Wembley, W.A. 6014.

Pregnancy and lactation result in a significant depression in wool growth in grazing ewes (Corbett 1979). The decrease in rate of growth during pregnancy has been estimated at between 20 and 45% and during lactation at 12–60% (Corbett 1979; Oddy 1985). With the decrease in wool growth, annual fleece weights are reduced. Oddy (1985) calculated that the deficit in clean wool produced during pregnancy and lactation (difference between observed wool growth and that expected on the basis of the relationship between feed intake and wool growth in dry ewes) ranged from 1.1 to 1.7 kg (depending on the type of diet). The range of reports cited by Corbett (1979) indicate a decrease in annual clean fleece production of 1 to 9.5%.

Recently the quality of wool produced has become of increasing importance. Quality is influenced by a number of raw wool characteristics including fibre diameter, staple length, staple strength and the point of break (or weakest point) in the wool. Pregnancy and lactation results in decreases in average diameter of up to 1.5 microns, in tensile strength of up to 30 N/ktex and in staple length of up to 9 mm (Masters and Stewart 1990). The changes in staple strength, in particular, may be severe, with a depression of up to 50% (Hansford and Kennedy 1988) and a consequent increase in tender fleeces. These changes in wool growth and quality may be amplified when a ewe rears twins or triplets. However, the limited evidence available indicates that the cumulative decline in fleece weight and fibre diameter, but not staple strength, resulting from the production of twins or triplets is much less than the sum of the losses expected from the production of two or three single lambs (Croker *et al.* 1990). Reduction in fleece weight, staple strength and length are, therefore, costs associated with producing lambs but the reduction in average fibre diameter is of benefit.

Management strategies to minimise negative effects of pregnancy on wool production

The aim of any management strategy for reproducing ewes should be to maintain the value of raw wool grown by minimising the depression in staple strength without significantly increasing average fibre diameter. This may be possible as wool growth falls rapidly towards the end of pregnancy and may increase in early lactation (Hansford and Kennedy 1988). The point of minimum fibre diameter may then be restricted to a short and identified time period. Alternatively management practices may be adopted that decrease the number of breeding ewes required.

Nutrition

The feeding of supplements, such as lupin seed or oats, during late pregnancy has not consistently resulted in increased staple strength or wool growth (Ralph 1984). These supplements do not appear to provide the nutrients that are limiting wool growth at this time. However, supplements containing protected proteins do increase wool growth in the last 3 weeks of pregnancy (Masters and Stewart unpublished data). Similar amounts of protein, supplied as lupin seed do not prevent a decline in wool production (Fig. 4). Although fishmeal is more expensive than lupin seed, it contains twice as much protein and this is used more efficiently for wool growth. In the experiment cited, staple strength was not significantly increased (30.4 and 34.5 N/ktex for lupin and fishmeal groups) and further research is required to determine if feeding such supplements will increase staple strength when tender wool (< 20 N/ktex) is expected.

Increase fecundity

As the penalty, in depressed wool production, is not doubled when a ewe rears twins rather than a single lamb, using twin-producing ewes may minimise the loss in wool production by decreasing the proportion of each flock required for the production of replacement sheep. However, the limited data available indicate that the penalty in reduced staple strength is doubled by the production of more than one lamb (Croker *et al.* 1990) and this strategy may need to be used together with improved nutrition.

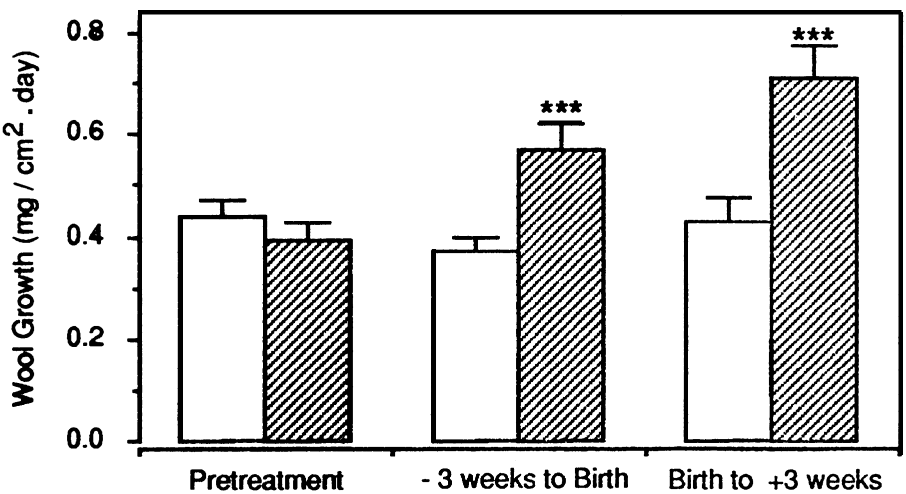

Fig. 4. Wool growth in late pregnancy and early lactation in ewes fed lupins (open bars) or fishmeal (hatched bars). Vertical bars represent s.d. (***P < 0.001).

Management of shearing and lambing times

By timing shearing so that it is close to the weakest point in the staple or by changing time of lambing to a period of more abundant feed, the depression in staple strength can be avoided while the benefits of reduced diameter during pregnancy and lactation can be partially retained. However, later lambing is often not favoured, particularly in mediterranean regions, because lambs have insufficient time to grow before the summer drought and small lambs are susceptible to eye damage from grass seeds. In the same climatic zones, there are also disadvantages to a change in shearing time because of the inverse association between tenderness and vegetable fault (Arnold and Gordon 1973). Shearing near lambing (in autumn) will reduce tenderness but cause a higher proportion of vegetable contamination.

ECONOMIC ASSESSMENT OF INCREASED REPRODUCTION

C. M. OLDHAM[A] *and J. M. YOUNG*[B]

[A]Dept of Animal Science and Production, University of Western Australia, Nedlands, W.A. 6009.
[B]Western Australian Dept of Agriculture, Katanning, W.A. 6317.

It is theoretically possible to increase farm profit by increasing reproductive rate (Young *et al.* 1990). The increase in profit achieved varies with the stocking rate, time of lambing, flock structure, genetic selection programs and the technique used to increase weaning percentage.

Comparing the costs and benefits suggests that only techniques with a low cost per unit increase in weaning percentage will be profitable to adopt. The costs of the techniques examined (Table 2) varied from no cost to $A3.50 per 10% increase in weaning percentage per ewe present ($/10%/ewe). This compares with a benefit that ranged from –$0.74/10%/ewe to +$2.50/10%/ewe. An additional $1.50/10%/ewe is possible if a selection program based on economically important traits is operating. An increase in profitability of $2.50/10%/ewe translates as an increase in whole farm profitability of about 10%. Techniques used to increase reproductive rate may have both direct costs and indirect costs related to foregone income. Estimates are likely to vary greatly between regions and between farms but they give approximate figures against which the benefits can be compared.

While a 10% increase in profitability is substantial, gains in farm profitability from increased reproductive rate were sensitive to the absolute and relative prices of wool and meat. Further, the prices of output would fall if the industry increased output as a result of increased reproductive rate (Young *et al.* 1990). Thus the challenge is to incorporate techniques for increased reproductive rate that are low cost while at the same time remaining sensitive to price signals from the market place for all outputs.

Table 2. Costs expressed as dollars per 10% increase in weaning percentage per ewe present ($/10%/ewe), of a number of strategies for increasing 'reproductive performance' of Merino flocks (taken from Young *et al.* 1990)

Strategy	Site of action	Cost ($/10%/ewe)
Feeding lupins at mating	Twinning rate	3.50
Feeding lupins at a synchronised mating	Ewes lambing and twinning rate	0.90
Grazing lupin stubble	Ewes lambing and twinning rate	—
Increased liveweight at joining	Ewes lambing and twinning rate	2.40
Immunisation against steroids	Twinning rate	0.54
Breeding (Booroola genes)	Twinning rate	0.25
Increased lamb survival	Lambs weaned of lambs born	?

An increase in the 'Reproductive Performance' of a Merino sheep enterprise can be used to increase farm profits through increased outputs and decreased cost. The increase in profit is not as direct as that achieved from an increase in wool production and generally occurs after the effects of the higher reproductive rate has worked through the whole flock. This has 2 ramifications, firstly, once-off high lambing performance will not accrue all the benefits of sustained high reproductive rate and secondly, effects do not accrue in the year that the high reproductive rate is achieved. The benefits may be spread over 4 or 5 years and may not be obvious in any 1 year.

Reproductive performance of a flock can be increased by increasing all or 1 of the following: (i) serving capacity of rams (the number of rams per ewe joined); (ii) fertility (the number of ewes lambing per ewe joined); (iii) prolificacy (the number of lambs born per ewe lambing); (iv) lamb survival (lambs weaned per lambs born).

The mechanisms by which higher reproductive rate can increase farm profit are:

(i) Changed flock structure and wool production. A flock with a higher weaning percentage requires fewer ewes to produce sufficient replacement stock to maintain the flock.' Because ewes generally produce less wool than wethers, reducing the proportion of ewes leads to an increase in total wool production. Also, because there are more young sheep in the flock a higher proportion of the wool grown is from hoggets. This increases profit because hoggets' wool is more valuable, because of its finer fibre diameter;

(ii) *Increased sheep turn-off.* If flock size is held constant a flock with a higher reproductive rate has more animals for sale in total. There is an increase in turn-off of high value surplus ewe hoggets and wethers but a reduction in turn-off of low value cast-for-age ewes;

(iii) Increased selection pressure on replacement ewes. The increased selection pressure can lead to increased production because the animals selected will perform better during their lifetime (phenotype) and also their progeny will on average perform better (genotype). To benefit from increased selection pressure the breeding program must be based on economically important traits;

(iv) Increased flexibility and potential for flock build up. In the past this has not been highly valued but a high reproductive rate would be valuable to farmers rebuilding flocks after a drought.

(v) Reduced ram numbers. The average ram percentage used is about 2.5% and except for fully synchronised joining this is adequate (Cameron and Tilbrook 1990). At $250 per flock ram and 1% versus 2.5% rams the saving of $375 per 100 ewes joined at $3.75 per ewe joined is substantial. The economic risk associated with a lower reproductive performance is low and the economic value of an increased selection differential among the rams used may be high.

There are also factors that may reduce these advantages:

(i) The size of the flock is limited by availability of feed. This is self evident, but it means that the changes to flock structure that can be implemented as a result of an increase in 'reproductive efficiency' only involve trade-offs between classes of animals. If only fertility is increased, the number of dry ewes carried is reduced and the number of reproducing ewes, wethers and young sheep is increased. However, if the twinning rate and lamb survival are increased there would be a reduction in the number of reproducing ewes which should reduce the overall cost per lamb weaned.

(ii) Reproducing ewes grow less wool per unit of feed consumed than dry sheep. Thus, a flock with a high proportion of pregnant ewes will have depressed wool production relative to a flock with a lower reproductive rate. However, under paddock conditions the penalty for a ewe weaning multiple lambs versus flockmates weaning a single lamb is not clear (Masters and Stewart 1990).

REFERENCES

ARNOLD, G. W., and GORDON, I. D. (1973). *J. Aust. Inst. Agric. Sci.* 39: 151–155.

BLOCKEY, M. A. de B., and WILKINS, J. F (1984). *In* 'Reproduction in Sheep' (Eds D. R. Lindsay, and D. T. Pearce.) p. 53 (Australian Academy of Science Press, Canberra.)

CAMERON, A. W. N., and TILBROOK, A. J. (1990). *In* 'Reproductive Physiology of Merino Sheep-Concepts and Consequences' (Eds C. M. Oldham, G. B. Martin and I.W. Purvis.) p. 13 1 (School of Agriculture, University of Western Australia: Perth.)

COGNIE, Y., GRAY. S. J., LINDSAY, D. R., OLDHAM, C. M., PEARCE, D. T., and SIGNORET, J. P. (1982). *Proc. Aust. Soc. Anim Prod. 14: 5* 19-22.

CORBETT, J. L. (1979). *In* 'Physiological and Environmental Limitations to Wool Growth' (Eds. J. L. Black and I? J. Reis.) p. 79 (The University of New England Publishing Unit: Armidale.)

CROKER, K. P., JOHNS, M. A., BELL, S. H., BROWN, G. A., and WALLACE, J. F. (1990). *Aust. J. Exp. Agric.* 30: 469-76.

CROKER, K. P., JOHNS, M. A., and JOHNSON, T. J. (1985). *Aust. J. Exp. Agric. Anim. Husb. 25:* 21.

DONNELLY, J. R. (1984). *Aust. J. Agric. Res. 35:* 709-21.

HANSFORD, K. A., and KENNEDY, J. *F?* (1988). *Proc Aust. Soc. Anim. Prod.* 17: 415.

KING, C. F. (1976). *Proc. Aust. Soc. Anim. Prod.* 11: 12 1.

KING, J. M., FISHER, J. S., and MURPHY, *F?* M. (1990). *Proc. Aust. Soc. Anim. Prod.* 18: 272.

KNIGHT, T. W., OLDHAM, C. M., SMITH, J. F., and LINDSAY, D. R. (1975). *Aust. J. Exp. Agric. Anim. Husb.* 15: 183.

LINDSAY, D. R., GHERARDI, P. B., and OLDHAM, C. M. (1976). *In* 'Sheep Breeding' (Eds G. J. Tomes, D. E. Robertson and R. J. Lightfoot.) p. 294 (Western Australian Institute of Technology Press, Perth.)

LINDSAY, D. R., KNIGHT, T. W., SMITH, J. F., and OLDHAM, C. M. (1975). *Aust. J. Agric. Res. 26:* 189.

LINDSAY, D. R., MARTIN, G. B., and WILLIAMS, I. H. (1991). World Review of Animal Production. (In press).

MARTIN, G. B., OLDHAM, C. M., COGNIE, Y., and PEARCE, D. T. (1986). *Livestock Prod. Sci.* 113: 219.

MASTERS, D. G., and STEWART, C. A. (1990). *In* 'Reproductive Physiology of Merino Sheep. Concepts and Consequences' (Eds C. M. Oldham, G. B. Martin and I. W. Purvis.) p. 265 (School of Agriculture, University of Western Australia: Perth.)

MORLEY, F. H. W., WHITE, D. H., KENNEY, P. A., and DAVIS, I. F. (1978). *Agric. Syst. 3: 27.*

ODDY, V. H. (1985). *J. Agric. Sci.* **105:** 613-22.

OLDHAM, C. M., LINDSAY, D. R., and MARTIN, G. B. (1990). *In* 'Reproductive physiology of Merino sheep — Concepts and Consequences' (Eds C. M. Oldham, G.B. Martin and I. W. Purvis.) p. 41 (School of Agriculture: University of Western Australia, Perth.)

PEARCE, D. T., and OLDHAM, C. M. (1984). *In* 'Reproduction in Sheep' (Eds D. R. Lindsay and D. T. Pearce.) p. 26 (Australian Academy of Science Press, Canberra.)

PEARCE, G. P., and OLDHAM, C. M. (1988). *J. Reprod. Fert.* 84: 333-9.

RALPH, I. G. (1984). *Proc Aust. Soc. Anim. Prod.* **15: 549-52.**

SCARAMUZZI, R. J. (1988). *Proc. Aust. Soc. Anim. Prod.* **17: 57.**

STEWART, R., and OLDHAM, C. M. (1986). *Proc. Aust. Soc. Anim. Prod.* **16: 367.**

YOUNG, J. M., HERTZLER, G., and OLDHAM, C. M. (1990). *In* 'Reproductive Physiology of Merino Sheep — Concepts and Consequences' (Eds C. M. Oldham, G. B. Martin and I. W. Purvis.) p. 289 (School of Agriculture, University of Western Australia: Perth.)