

MANIPULATION OF REPRODUCTION OF SHEEP AND CATTLE BY
PHARMACOLOGICAL, MANAGEMENT AND GENETIC METHODS

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I. INTRODUCTION

Ultimate control of reproduction of farm animals may involve manipulation of the frequency of conception, number of offspring per conception, and the genotype, including the sex of the offspring. Such manipulation will require major advances in research and application of reproductive biology.

This review deals with the present state of knowledge of methods concerned with control of reproduction in the sheep and cattle industries of Australia. Most emphasis will be placed on recent advances in those areas of research likely to find relevance to the Australian animal production scene. There is a large and expanding volume of literature in this field. To keep references to a minimum review articles have been referred to where possible. The author concedes that some key references have been omitted.

Some aspects of this subject have been reviewed for this Society in the past (Robinson and Lamond 1966; Restall 1970). More recently a surfeit of review articles dealing with control of reproduction has appeared. Of special significance are those by Rowson (1971), Hansel (1972), Jöchle (1972), Robinson (1972), and Polge and Rowson (1973). An excellent, comprehensive analysis of the reproductive biology of cattle and sheep in Australia has been prepared by Braden & Baker (1973).

This review deals mainly with factors affecting fertility (i.e. the ability to conceive) and fecundity (i.e. the number of offspring per conception). Survival of offspring and reproduction in the male will not be considered.

II. MANIPULATION OF FEMALE REPRODUCTION

(a) Pharmacological techniques

(i) Limitations to use of Pharmacological agents

Compounds potentially useful for controlling reproduction include natural and synthetic hormones and their analogues, as well as a variety of chemicals resulting from the expanding research of pharmaceutical firms. Apart from being of proven effectiveness and reliability, such compounds must also comply with legislative restrictions governing the administration of any drug to animals producing food for human consumption.

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State legislation in this matter is guided by recommendations of the Technical Committee on Veterinary Drugs (TCVD) in the Commonwealth Department of Primary Industry.. This committee bears responsibility for evaluating drugs proposed for mass medication of farm animals. Part of this evaluation may involve adherence to standards laid down by nations importing our edible livestock products.

Two points are important here. Pharmacological agents for controlling reproduction of livestock are unlikely to be approved in Australia if their use is not permitted in countries importing Australian meat. Secondly, present laws permit only veterinarians to use hormones with animals; administration by the farmer would require a major change in policy.

(ii) Increasing the opportunities for conception

Reproductive efficiency may be improved by increasing the occurrence of oestrus. This can be done by the induction of precocious puberty and by elimination of seasonal and post-partum anoestrus.

Administration of progestational steroids followed by gonadotrophin (commonly PMSG) induces ovulation from as early as eight weeks of age in sheep and calves; animals treated at this age do now show oestrus or commence regular oestrous cycles (Jöchle 1972). Hormonal acceleration of puberty in sheep and cattle is not sufficiently reliable to allow commercial application. Delayed puberty in dairy heifers in sub-tropical Australia has been interrupted by treatment with progesterone and PMSG (Hewetson 1968).

Seasonal anoestrus does not appear to pose a problem with cattle, but must represent the single most important, recurrent factor limiting the manipulation of reproduction of Australian sheep. Almost a decade ago Australian research (Robinson 1964) provided a major advance in pharmacological techniques to overcome seasonal anoestrus of sheep. The intravaginal progestagen pessary, coupled with an injection of PMSG, now finds commercial application in Ireland (Gordon 1973) and Europe (Robinson 1972) for advancing the breeding season of sheep. It seems fair to say that this technique would be a practical reality in the Australian sheep industry today if the appropriate research had received continuing support during the period when economic factors in the industry made the method unattractive. It is possible that two lambings per year could now be achieved by the combined use of the progestagen pessary and agents that cause the induction of LH release and ovulation. These include oestrogens (Goding et al. 1969), androgens (Radford and Wallace 1971) and gonadotrophin releasing hormone (GnRH) (Cumming et al. 1972).

Attempts at interruption of post-partum anoestrus of sheep by pharmacological means have been many and varied. Most studies have been based on a period of about 2 weeks progestagen treatment, followed by an injection of PMSG. Of about 32 such studies (involving many breeds in several countries) reviewed by Hunter (1968) only eight yielded 50% success (i.e. ewes lambing of ewes treated) and none equalled normal fertility. More recent tests have been no more successful (see Robinson 1972). The work of Pelletier and Thimonier (1973) points to reduced synthesis and release of LH by the lactating ewe. Perhaps this deficiency is responsible for the poor results with post-partum ewes?

Analogous studies in cattle have aimed at a post-partum anoestrus shorter than 90 days, so that each cow may produce one calf per year. The problem appears more pressing in beef than dairy cattle, more pronounced in B. indicus than B. taurus types, and is accentuated by undernutrition (Baker 1969).

As in sheep, the pharmacological requirements are clearly defined: it is necessary to subject the cow to a period of progestational steroid and gonadotrophin treatment which will be followed by oestrus and ovulation; fertility must be normal and lactation unimpaired. Recent reviews (Jöchle 1972; Hansel 1972) suggest that a regularly successful pharmacological treatment is not available to achieve this.

(iii) Synchronization of oestrus

Benefits from synchronization of ovarian cycles have been stated often enough (Lamond 1964; Robinson and Lamond 1966). Presently there is no great need for synchronization in the Australian sheep industry, except in conjunction with ovum transfer and artificial insemination, if these become popular. In beef cattle the expanding use of artificial insemination of imported semen and the desire to eliminate venereal diseases provide a continuing demand for successful synchronization.

The present review need only examine recent developments. Synchronization based on progestational steroids has been successfully applied to the sheep industries of Britain and France by using the intravaginal pessary (Robinson 1972). A similar pessary for use in cattle has been tried (Carrick and Shelton 1967; Smith 1974), but with variable success owing to poor retention of pessaries in heifers and reduced fertility after pessary removal. The technique merits further investigation. Progestagens have also been given to cattle in the feed, in the water, by injection and as implants. The review of this work by Hansel (1972) leaves the impression that none of these procedures is entirely successful. Despite 13 years of research none of these methods is used in commercial cattle breeding.

Synchronization can also be achieved by causing regression of the corpus luteum. Oxytocin, anti-bodies to LH and prostaglandins can be used to this end. Australian scientists (Goding et al. 1972; Thorburn et al. 1972) played an important part in demonstrating prostaglandin F_{2α} (PGF_{2α}) as the luteolytic hormone in the sheep. This substance has now been shown to synchronize oestrus effectively when administered at any time during days 5 to 16 of the cow oestrous cycle (Rowson, Tervit and Brand 1972). It is effective via the intra-muscular, intravaginal or intrauterine routes (Louis, Hafs and Seguin 1973) and new synthetic analogues of PGF_{2α} promise added potency and ease of administration (Tervit, Rowson and Brand 1973).

If these substances prove reliable and without serious side effects they may stimulate renewed interest in controlled breeding of beef cattle.

(iv) Increasing the number of offspring per conception

Artificial increases in litter size may be achieved by increasing the number of ovulations or by transfer of extra embryos into the uterus. Both procedures are greatly simplified if oestrus and ovulation can be reliably synchronized.

The most urgent need is for a pharmacological agent that will reliably cause exactly two ovulations in sheep and cattle. There is no doubt that farmers would welcome temporary increases in fecundity by such means; there is also little doubt that farmers wish to avoid litter sizes greater than two. Present techniques cannot guarantee this. Administration of PMSG during the oestrous cycle of the ewe and cow produces results that are notoriously variable. Crude or purified extracts of pituitary tissue have been more successful, but regulation of the response to two ovulations is not possible. Synthetic GnRH causes prompt release of LH in the ewe (Reeves, Arimura and Schally 1970) and cow (Zolman et al. 1973). In the ewe, however, GnRH administration on days 11 & 12 of 1

oestrous cycle or the morning of the day of oestrus does not increase ovulation rate, despite demonstrable increases in LH (B.M. Bindon, unpublished). One chemical substance, unrelated to gonadotrophin, capable of increasing ovulation rate is cyclophosphamide (Russell, Walpole and Labhsetwar 1973). Testing of this in livestock is awaited with interest.

Recent developments in the field of embryo transfer have been reviewed by Polge and Rowson (1973). The induction of "artificial" twinning in cattle by this means is a most attractive proposition. The lack of reliable methods for producing large numbers of fertilized ova is a continuing problem, which may be resolved by new procedures for superovulation based on the use of PGF 2α and PMSG, collection of ova from slaughter-house material and in vitro fertilization and storage of ova (see Polge and Rowson 1973). A non-surgical method of embryo transfer is being sought (Sugie et al. 1971) and simplification of existing surgical methods is being investigated (Bedirian & Baker 1973). Commercial application of the embryo transfer technique is not common at present in Australia for either sheep or cattle.

(v) Artificial reduction of gestation length

Parturition may be advanced by a single injection of corticosteroid in sheep (Bosc 1972) and cattle (Lauderdale 1972). This procedure is used in France to synchronize lambing in ewes and is now widely utilized in New Zealand (Welch 1973) to achieve concentrated calving of dairy cattle to simplify their nutritional management. Approximately 5% of the national herd was treated in 1972/73. The serious calf mortality (up to 35% in the New Zealand study) would be prohibitive for the Australian dairying industry, but further research may eliminate this and other side effects. The method is not presently used in the Australian sheep industry.

(b) Management techniques

In the context of this review management methods include those procedures of husbandry nature that are available directly to the farmer. Nutritional, seasonal and climatic effects on reproduction can all be manipulated. Some procedures provide guaranteed benefits; others produce less reliable effects.

(i) Nutritional effects

Manipulation of animal nutrition is an alternative always available to the farmer. Undernutrition of sheep and cattle is associated with delayed puberty, reduced conception rates, low fecundity and increased seasonal and lactation anoestrus (see reviews by Lamond 1970; Braden and Baker 1973). It is more difficult to define the positive or beneficial aspects of an increased level of nutrition on animal reproduction.

There is a well established association between pre-mating live weight of the ewe and lambing performance (Killeen 1967; Edey 1968; Lax and Brown 1968; Suiter and Fels 1971). This so called "static" effect may be responsible for substantial improvement of both fertility and fecundity (Suiter and Fels 1971). Estimates of its importance in Merino sheep range from 3 to 8 per cent increase in twinning for each 10 lb increase in pre-mating live weight.

The phenomenon of "flushing" or the sudden increase in the level of nutrition of previously undernourished ewes has been shown to exert its effect by increasing fecundity rather than fertility and may increase twinning by 10% (Coop 1966). The nutritional basis of flushing is not yet understood, nor is it known whether the effect is mediated via effects on the ovary or pituitary hormone secretion.

These phenomena provide obvious methods for manipulating sheep reproduction. Their fuller understanding may result in more reliable application by farmers. Research is required to separate the contribution of skeletal size and body condition to the liveweight effects on reproduction.

In cattle, regrettably, fecundity may not be increased by nutritional stimulation. Nutritional effects on other aspects of cattle reproductive performance include acceleration of puberty and increased fertility of heifers (Sparke and Lamond 1968), improvement of dairy cow fertility (McClure 1965) and variable effects on the fertility of beef cows (Wiltbank et al. 1964).

(ii) Photoperiod

It is theoretically possible to alter the photoperiod in such a way as to eliminate or reduce seasonal anoestrus in sheep.

At Aberdeen, Robinson, Fraser and Gill (1972) are examining the combined effects of controlled photoperiod, synchronization of oestrus, early weaning of lambs and regulation of nutrient intake on the performance of ewes of high reproductive potential (Finnsheep x Dorset Horn crossbreds). These animals have lambed at intervals of 8 months with consistently high fertility and fecundity.

Such intensification of sheep husbandry is not presently practised in Australia. More benefit could arise if renewed research effort were applied to solving the mystery of how the light environment is able to turn sheep ovarian cycles on and off with such precision.

(iii) Breeding schedules

Efficiency of reproduction may be improved by altering time of joining, or the number and time of introduction of males, by use of pregnancy diagnosis or by early weaning.

There is evidence of seasonal variation in ovulation rate of the Australian Merino (reviewed by Braden and Baker 1973). A joining period coinciding with highest ovulation rates should be beneficial. Identification of this time is not easy however, nor can it be reliably predicted. In the absence of nutritional and climatic stress, there does not appear to be seasonal variation in fertility and cattle.

Introduction of the ram may advance the start of the breeding season (Schinckel 1954) and may also reduce the length of the post-partum interval to ovulation (Hunter, Belonje and Van Niekerk 1970). Increasing the number of rams in the flock may increase fertility, especially where young rams (Lightfoot and Smith 1968) or young ewes (Connors and Giles 1970) are being joined. Some recent observations of cattle mating behaviour have been reported (Mattner, George and Braden 1974). Their significance for fertility are not yet known.

Pregnancy diagnosis in cattle offers immediate economic benefits (Duncan 1967). Pregnancy diagnosis of sheep is not widely utilized although techniques based on returns to service, palpation with a rectal probe, ultrasonic devices, x-ray and plasma progesterone levels are available (reviewed by Braden and Baker 1973). None of these methods is consistently effective in identifying ewes carrying more than one foetus.

Early weaning (i.e. 6 to 8 weeks after parturition) of calves is known to improve conception rates if the joining period is short (Laster, Glimp and Gregory 1973). Temporary calf removal was without beneficial effects on reproductive performance of cattle in Rhodesia (Symington 1969). There is some disagreement as to whether lamb removal hastens the onset of oestrus in sheep. Hunter and Van Aarde (1973) conclude that if lactating and non-lactating ewes are fed to meet their respective nutritional requirements, the length of their post-partum anoestrous periods will not differ.

(c) Genetic methods

(i) Advantages and disadvantages

Genetic methods cover selection of individuals within groups, or crossing of genetically distinct groups (strains or breeds), with or without heterosis. Selection for reproduction rate or its components is likely to be slow. Even the relatively rapid gains from crossing may be less attractive to the farmer than the "instant" increases in fertility or fecundity following drug injection or embryo transfer. Gains from selection or from crossing (in the absence of heterosis) are, however, permanent.

(ii) Genetic improvement of sheep reproduction

It is of interest to examine which contributing factors change when reproduction rate is altered by selection. This may reveal the scope for manipulation of reproduction by genetic means.

The subject has been extensively reviewed by Turner (1969), Bradford (1972) and Land (1974). Useful information is available from the results of within-breed selection for fecundity in the Merino (Turner 1969), the effects of crossbreeding and heterosis (e.g. Watson 1971) and comparisons between breeds in the one environment. In Table 1 the evidence for genetic differences in a number of reproductive phenomena of importance is summarized.

TABLE 1

Evidence for genetic effects (+, 0, or -) on key reproductive phenomena of sheep based on three types of genetic study.

<u>Reproductive phenomenon</u>	<u>Selection within breed \emptyset</u>	<u>Crossbreeding[*] with or with- out heterosis</u>	<u>Comparisons between breeds in one environment^{**}</u>
Age at puberty	+	+	+
Length of breeding season	+	Not available	+
Duration of oestrus	0	"	+
Ovulation rate	+	+	+
Conception rate	0	+	0
Length of <u>post-partum</u> anoestrus	0	+	+
Libido of ram	+	Not available	+

Ø Based on data of Turner (1969), Bindon et al. (1971) and unpublished data from CSIRO Animal Genetics.

* Based on data of McGuirk (1967); Watson (1971); and others.

** See Land (1974) for details.

This summary suggests that when a character such as litter size is increased by selection or crossing, other characters important for reproduction rate will also be improved. Table 1, of course, does not reveal the **rate of** progress that might be made by genetic means. Such information is scarce, although recent reviewers of within-breed selection for litter size (Turner 1969; Bradford 1972) indicate an annual increase of between 0.017 and 0.023 lambs per ewe. This may be too low to attract farmers wanting short term benefits. On the other hand crossing (even without heterosis) based on highly fecund Merinos or exotic breeds such as Finnsheep or the Romanov should provide substantial and rapid improvement in fecundity and possibly the other components shown in Table 1.

Heterosis may be responsible for spectacular increases in reproduction rate (e.g. see Turner 1969). The awareness and ready acceptance of the phenomenon by farmers is attested to by the popularity of the Merino x Border Leicester Fl ewe as the basis of eastern Australia's fat lamb industry.

(iii) Genetic improvement of cattle reproduction

There is little evidence of genetic differences in cattle reproductive performance in Australia. Breed comparisons in Britain (M.L.C. Study Group Report 1971) and Europe (Mason 1971) lead also to the conclusion that there has been little genetic divergence in reproductive traits of the world's major breeds.

Crossbreeding, however, has been shown to offer important benefits for cattle reproduction rate. A major comparison involving crosses of Angus, Hereford and Shorthorns in the United States (summarized by Gregory 1971) showed that at least half of the 25% productive advantage of crossbreds was due to heterosis in the reproductive performance of crossbred dams. An interesting feature of this study was the demonstration of a significant heterotic effect on age at puberty, independent of effects due to increased growth.

There is no reason to suppose that such improvement in cattle reproduction is not possible in Australia by immediate crossbreeding of indigenous breeds. No doubt this **procedure** is already in commercial use, even if local experimental evidence for its existence is unavailable.

No adequate attempt has yet been made to increase fecundity in cattle by genetic means (Hendy and Bowman 1970), while both conscious and unconscious selection against the phenomenon has been traditional. The sterility of heifer calves born co-twin to a male (i.e. freemartins) may be responsible for this attitude. However these are easily identified and are ideal for meat production. Despite freemartinism, cattle twinning yields the same number of fertile heifers for selection as in herds' producing single births.

The lack of a highly fecund breed of cattle represents a major world deficiency when one considers that cattle of almost every colour, size, shape, growth rate and milk production are available on the international market. A specialized dam line or breed with twinning as a major trait could

make an important contribution to crossbreeding programmes for areas of Australia where nutrition is not a limiting factor.

(iv) Hormone measurement as an aid to selection for reproduction rate

The relatively slow response to within-breed selection for ewe fertility and fecundity has stimulated research on the hormonal basis of genetic differences in them. The idea is simple. If one could measure the hormones responsible for these characters, then perhaps one could discriminate between individuals more accurately than by measuring the character itself. To be of any value in selection, the heritability of the hormone measurement would have to be higher than that of the character itself and the genetic correlation between the two must also be large.

Both CSIRO and the Animal Breeding Research Organization in Edinburgh are studying this approach. In the CSIRO study the main point to emerge has been the demonstration (Bindon 1973) that young male and female lambs from groups selected for fecundity have higher plasma LH. In the study based on the Finnsheep and its crosses (Land 1974) differences in testis growth, (also reflecting LH activity), appear to be the most useful early indicator of fecundity. The value of both types of measurement, at least in genetic terms, has yet to be evaluated.

III. DISCUSSION

This review leaves the impression that there are few reliable methods for manipulating reproductive performance. Hormonal techniques have yet to reach the stage where they could be confidently recommended. Progress from within-breed selection for reproduction rate is also likely to be too slow to be used by individual farmers. On the other hand crossing with high fecundity Merinos and exploitation of heterosis in reproduction rate of sheep and cattle should provide useful and fairly rapid benefits.

Of the management methods available, pregnancy diagnosis in cattle and exploitation of the beneficial effects of nutrition on sheep reproduction can both be recommended.

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