TIMING AND FREQUENCY OF REPRODUCTION IN SHEEP - PHYSIOLOGICAL FACTORS

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RESUME

Le choix du moment et du rythme de reproduction suppose le contrôle de la production spermatique et de son utilisation d'une part et la possibilité d'induire oestrus et ovulation d'autre part. Il est possible d'agir sur la production spermatique en modifiant l'environnement photopériodique. En particulier, l'alternance de jours long et de jours courts tous les mois provoque le maintien d'un poids testiculaire (et donc d'une production spermatique) élevé tout au long de l'année. Il est aussi possible d'avancer la puberté chez des jeunes mâles par des traitements photopériodiques appropriés. Une complémentation alimentaire (lupin) avant la lutte induit également une croissance testiculaire. La production spermatique peut être utilisée par insémination artificielle ou naturelle. En particulier, les inséminations intra-utérines autorisent l'utilisation d'un faible nombre de spermatozoides ($25x10^6$ spermatozoides pour une fertilitée normale. Compte tenu de la production spermatique, de la fréquence des saillies, du comportement des béliers, il est possible de définir les conditions optimales d'utilisation des mâles. Dans les conditions extensives, des béliers Mérinos bien préparés à la lutte peuvent être utilisés dans la proportion de 1 mâle pour 100 brebis. Il est possible d'induire oestrus et ovulation par un traitement progestagène + PMSG pendant l'anoestrus saisonnier. Le traitement doit cependant être adapté à chaque condition d'élevage. L'obtention de retours en oestrus chez les brebis non gravides est une difficulté. Des techniques de diagnostic de gravidité ont donc été mises au point. L'oestrus et l'ovulation peuvent être induits par effet mâle. L'efficacité de cette technique est limitée avec les races ayant une saison de reproduction très marquée. L'injection de 20 mg de progestérone lors de l'introduction des béliers dans le troupeau induit une bonne synchronisation des oestrus 18 à 21 jours plus tard et permet l'insémination artificielle. L'administration de mélatonine (implant) avance dans certaines limites, le début de la saison de reproduction de 1 à 2 mois. Le système le plus répandu dans les cas d'augmentation de la fréquence des agnelages est probablement celui de 3 agnelages en 2 ans. Il met en oeuvre les techniques utilisables pour le choix du moment de mise à la reproduction.

RESUMEN

El escoger el momento y el ritmo de reproducción supone el control de la producción espermatica y su utilización, y por otro lado la posibilidad de inducir el estro y la ovulación. Es posible afectar la producción espermatica modificando el tratamiento fotoperiodico. La alternancia de los dias largos y de los dias cortos todo los meses provoca el mantenimiento del peso testicular, y por lo tanto una producción espermatica elevada todo el año. Es igualmente posible de avanzar la pubertad de los jovenes machos por tratamientos del fotoperiodo adecuados. Una complementación alimentaria (lupino) antes del servicio induce un crecimiento testicular. La producción de espermatozoides puede usada para la inseminación artificial o natural. En particular, las inseminaciones intra-uterinas permiten una utilización muy baja de espermatozoides (25×10^6) y el empleo de esperma congelado. En servicio natural hace falta por lo menos 60×10^6 espermatozoides para obtener una fertilidad normal.

Teniendo en cuenta la producción espermatica, la frecuencia de montas, la preferencia de los moruecos, se puenden determinar las condiciones optimas de utilisación de los machos. En condiciones extensivas, los moruecos Merino bien preparados para el servicio pueden ser utilizados en una proporción de 1 macho para 100 ovejas. Es posible inducir el estro y la ovulación con un tratamiento progestageno + PMSG durante el anestro estacional. Cada tratamiento debe estar adaptado a cada condición de cria. Las ovejas non gravidas que entran en anestro presentan cierta dificultad. Varias tecnicas de diagnostico de gestacion han sido peustas a punto. El estro y la ovulación pueden ser inducidos por el "effecto macho". La eficiencia de esta tecnica es limitada para algunas razas que tienen una epoca de reproducción muy marcada. La inyección de 20 mg de progesterona a la introducción de los machos en los rebanos induce una buena sincronización de los estros 18 a 21 dias más tarde y permitiendo la inseminación artificial. La administración de melatonina (implantes) adelanta con ciertos limites el principio de la epoca de reproducción de 1 a 2 meses. El sistema mas usado en los casos de aumento de la frecuencia de partos de las ovejas es probablement el de 3 partos en 2 años y necesita de varias tecnicas para escoger el momento adecuado de la reproducción.

INTRODUCTION

There are two principal ways of improving the efficiency of reproduction in sheep; increasing prolificacy through increasing multiple births, and changing the timing and the frequency with which flocks reproduce. This paper deals with the advantages and problems of controlling the time and frequency of reproduction.

Domestic sheep originated in Europe and almost all breeds show patterns of reproductive periodicity that confine lambing activity to the spring months when availability of forage and survival of lambs are likely to be high. These patterns are most pronounced in sheep from relatively high latitudes and are least pronounced in breeds that have been developed closer to the equator (Hafez 1952). Certainly, in mid-latitudes, all breeds show patterns of reproductive periodicity. There are obvious economic incentives to have sheep reproduce out of season. In meat-producing breeds lambs born at a time when lambs are scarce attract premium prices but, in addition, climatic conditions and availability of forage do not necessarily favour spring-born lambs in many countries. In Australia, for example, harsh summers and mild winters often favour autumn-born lambs which as a consequence must be produced at a time that is contrary to the physiological inclinations of the animals.

Most of the work over the last two decades on techniques for out-of-season breeding has concentrated on inducing ewes to ovulate and display oestrus but there is clear evidence that rams, specially those of breeds originating from high latitudes, also display marked seasonal variation in behavioural and spermatogenic capacity. This is illustrated for the Ile de France breed in Figure 1 (Ortavant et al. 1988)

THE RAM

Timing of reproduction

The major determinant of reproductive capacity in males is the photoperiod. For example, in the Ile de France breed the testicular weight of rams on a relatively constant diet may vary from as low as 190 g per testis in the spring to 300 g in the beginning of autumn (Pelletier 1971). Further, Ortavant (1958) showed that each gram of testis in the ram produces less spermatozoa per day in the spring (9.3×10^6) than in the autumn (12.2×10^6). Dacheux et al. (1981) were able to show that the net result of these differences between seasons resulted in almost five times as much spermatozoa being produced per testis in the autumn as in the spring (4.82×10^9 vs 1.02×10^9).

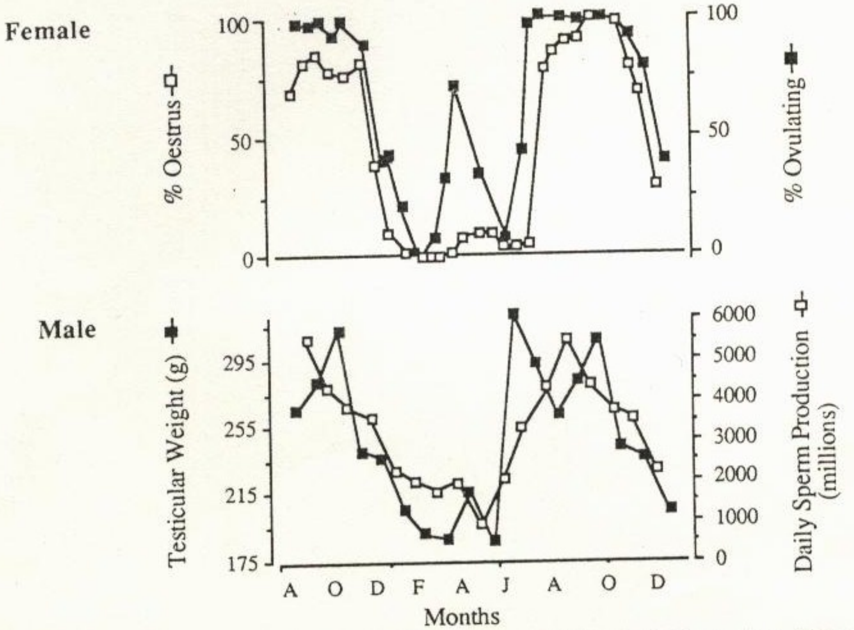

Figure 1 Seasonal variation in reproductive characteristics in male and female Ile de France sheep. (Taken from Ortavant et al. 1988)

The Ile de France can be considered an animal of the mid-latitudes and we might expect animals from higher latitudes to show even bigger differences than this between seasons. For genotypes developed in lower latitudes, for example the Australian Merino, differences between spring and autumn are not nearly so pronounced; Moule et al. (1966) showed that production of spermatozoa was higher in autumn than in spring but the differences were relatively small in animals kept on a constant feeding regime. Libido is also less variable between seasons in Merinos than in European breeds (Lindsay and Ellsmore 1967).

A further problem about the use of rams in the spring months is that the fertilising capacity of semen is likely to be lower than semen produced in the autumn. Colas et al. (1985) collected semen from rams subjected artificially to increasing or decreasing light and inseminated ewes in equal quantities with the semen collected. The lambing rate of ewes inseminated with semen from rams subjected to decreasing light was almost 10 percentage points higher than in ewes inseminated with semen from rams under increasing light (65.7 vs 56.7%). Thus there are many reasons why it is important to control the physiological responses of rams when considering out-of-season breeding.

Nutrition is also a major component in the capacity of rams to produce spermatozoa (Oldham et al. 1978). Under free-ranging conditions when nutrition is not controlled, it is even possible to demonstrate in the Merino breed that the nutrition of the animals can override the influence of photoperiod as shown in Figure 2 from Masters and Fels (1984), in which the testes were larger in late spring than in autumn, corresponding exactly to the availability of high-quality feed in the region in south Western Australia where these animals were run.

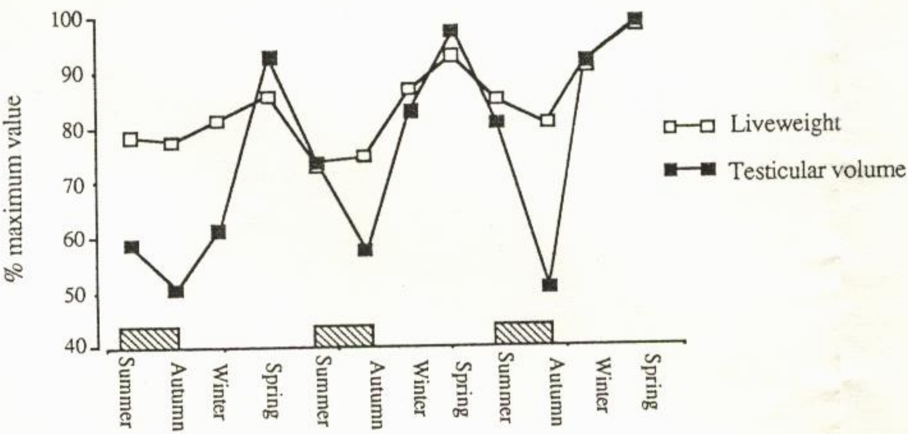

Figure 2 Seasonal changes in live weight and testicular volume of mature Merino rams (shaded areas indicate time of mating). (From Masters and Fels 1984)

Research into the timing of reproductive activity of rams in recent years has therefore followed two main paths. The first has been to attempt to reverse the deterioration in quality and quantity of semen resulting from increasing day length or from inadequate nutrition. The second has been to devise techniques that will utilise better the smaller quantities of spermatozoa produced by rams outside of their natural breeding season. Considerable progress has been made in both areas.

<u>The use of artificial light</u>

An obvious method of reversing the unfavourable consequences of increasing light is to reverse the light pattern itself. This system is now in use in AI centres in France and Colas et al. (1985) showed very clearly that rams can be induced successfully to produce large quantities of spermatozoa by subjecting them to decreasing light. Rams may be prepared by this method to produce semen at a desired time of the year regardless of its relation to the normal breeding season. The problem still remains, however, that there is a wide annual fluctuation in the capacity of rams to produce semen even though the timing of the peak production may be controlled. For the best use of rams a continual and reliable supply of semen throughout the year would be desirable.

The evidence suggests that the animal perceives the *change* in photoperiod rather than the absolute photoperiod and so it has been assumed that it would be impossible to maintain high productivity (e.g. large testicular size) for long periods and experiments in which rams have been subjected to constant day lengths regardless of the ratio of light and dark suggest that this is so. Nevertheless, recent results from Pelletier et al (1985) from experiments designed to prevent refractoriness to the stimulatory effects of short days have succeeded in reducing the magnitude of variation in testicular weight. In more recent experiments by Pelletier and Almeida (1987) the photoperiod was alternated every month from 16 h light and 8 h dark, to 8 h light and 16 h dark. This resulted in the testicular volume of rams increasing over the first six months and then remaining high for the next two years (Fig. 3).

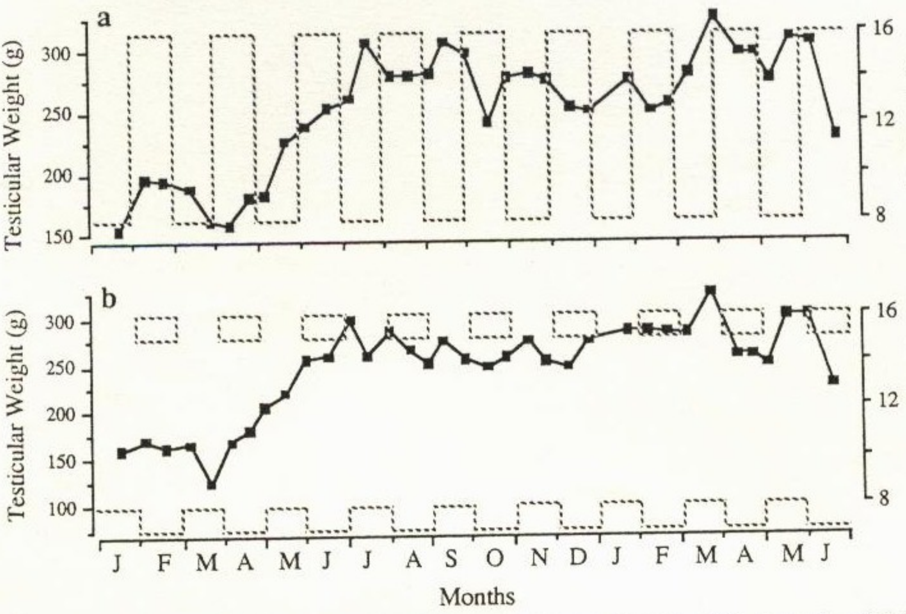

Figure 3 Testicular weight of rams exposed to (a) alternate months of short days (8 h) or long days (16 h); (b) 8 h of total daylength but on alternate months the 8th h was given 15 h after the initial dawn. (From Pelletier and Almeida 1987)

The timing of illumination was more important than the duration of illumination (Pelletier and Thimonier 1987). The same response was achieved by replacing long days by a "skeleton" photoperiod (7 h light, 8 h dark, 1 h light, 8 h dark). Not only were testicular volumes maintained but the semen production per ejaculate was comparable with that observed by Colas et al. (1985) for rams in the 'sexual season' and very significantly higher than that of rams in the 'non-sexual season'.

Thus, it is possible to maintain high levels of semen production throughout the year by manipulating the photoperiod. The significance of the 'flash' of one hour of light, 15-16 hours after the perceived dawn is that animals need not be kept in light conditioned rooms in order to achieve the effect of long days.

In young rams it is often desirable for genetic and economic purposes to have a reasonable production of semen in the first six or seven months of the animal's life. This shortens generation intervals, allows early progeny testing, and advances the time of use of valuable rams by 12 months. Beginning at three months of age Colas et al. (1987) treated animals to "long days" by giving them one hour of light, 16-17 hours after the dawn. Then they were given three months in which day-length was decreased gradually from 16 to 8 hours. In practice the "long day" treatment could be done outdoors with the "flash" being given at night, but decreasing day length has to be applied in light-proof buildings.

The light treatment successfully increased the testicular volume of young Ile-de-France rams over the controls so that by the age of 7-8 months the mean testicular volume of rams that had been treated was 198 ml vs only 105 ml for control animals. Rams of the Lacaune breed, which is considered to be less influenced by photoperiod than the Ile de France, had a significant, though less marked, increase in the volume of their testes over that of controls, and over twice as many doses of semen for artificial insemination were obtained from them.

A variation on the treatment designed to eliminate the necessity for light-proof buildings was to give two implants of melatonin subcutaneously at an interval of 65 days. This was designed to substitute for the decreasing day length.

Preliminary results for the melatonin treatment (G. Touré, G. Almeida, Y. Guérin and G. Colas, cited by Chemineau et al. 1988) suggest that it is less effective than the use of light treatments but is considerably better than relying on natural day length. The results are encouraging enough to attempt to use melatonin in other combinations of doses and timing to achieve more pronounced results.

Where nutrition of rams is not constant and subject to seasonal variation in quality and quantity, supplementary feeding may be necessary, to have rams in top reproductive capacity to coincide with natural joining or with artificial insemination programmes. Lindsay et al. (1977) showed that the capacity of rams to produce spermatozoa could be increased dramatically by a simple high-quality supplement of lupin grain (Fig. 4).

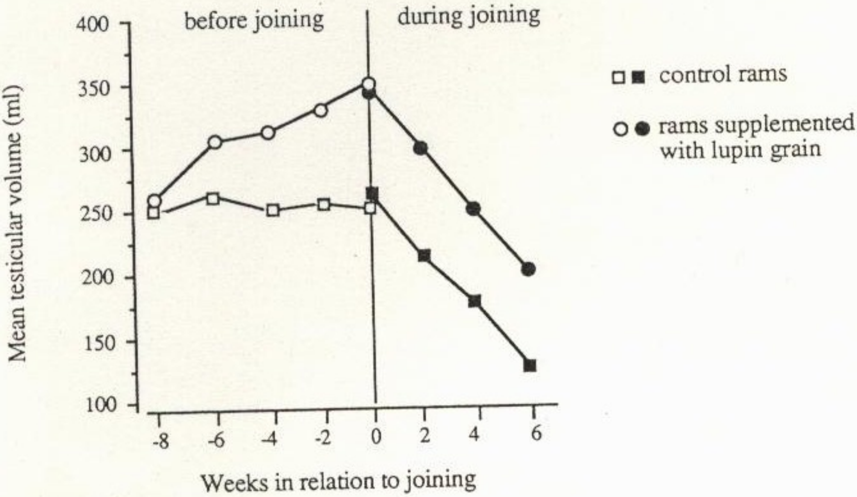

Figure 4 Changes in mean testicular volume of rams fed lupin grain before joining

Efficient use of small quantities of semen

A major advance in the efficient use of rams, especially out of season, has been the advent of laparoscopic insemination (Killeen and Caffery 1982). It involves the use of laparoscopy to deposit semen directly into the uterus. By bypassing the cervix this technique allows successful insemination with as little as 25×10^6 spermatozoa, only about one-tenth the quantity that would be considered normal for standard insemination (Maxwell 1986). Even more importantly, laparoscopic insemination of frozen semen results in normal fertility, something that has hitherto been impossible with standard doses of unselected frozen semen using conventional techniques. This introduces a strong degree of flexibility in the timing of the production of semen by rams where artificial insemination is used. Semen can be collected at the time of the year when production is most prolific, and fertility is highest. It can then be frozen, and used at any other time of the year appropriate to a desired breeding programme. In addition, young rams of 6-7 months of age producing small quantities of spermatozoa can still be used over relatively large numbers of ewes.

Frequency of breeding in rams

The ram has a very high ratio of testicular-to-body weight which indicates that it is capable of very high reproductive activity, at least for short periods (Lindsay 1988). With the introduction of synchronised joining and the exploitation of the genetical advantage of using high-quality rams as widely as possible, this attribute has taken on increasing importance in recent years. The number of spermatozoa per ejaculate in naturally joined rams is extremely sensitive to the number of ejaculates per day and the number of days that the ram has been working (Fig. 5).

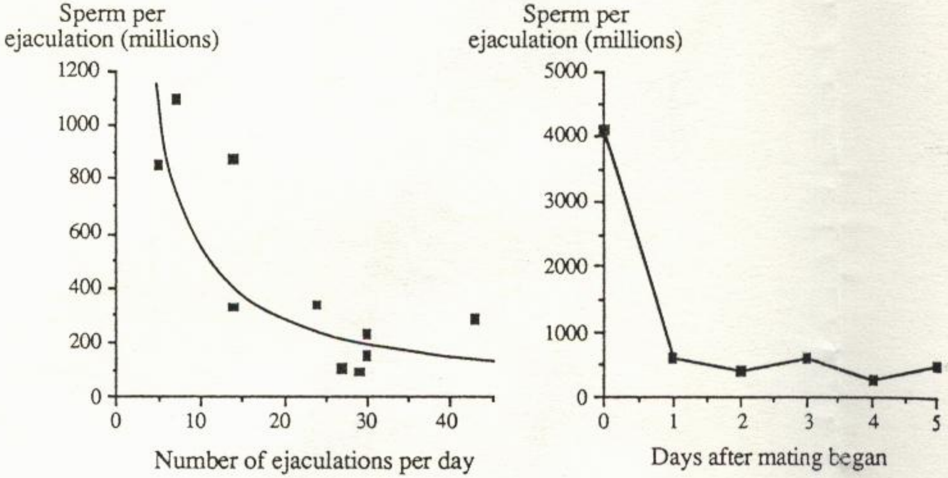

Figure 5 Relationship between the numbers of spermatozoa per ejaculation and the activity of naturally mated Merino rams. (From Cameron 1987)

Both the short-term and the long-term maintenance of spermatogenic activity is often important in sustained AI programmes. Cameron (1987) compared collections taken once, twice, four times, and eight times daily from Merino rams and measured their total output of spermatozoa. He found (Fig. 6) that collections made twice a day resulted in the maximum yield of spermatozoa per ram as well as ensuring reasonable sized individual ejaculates for processing. Some highly selected rams are used regularly for four or five months in some AI programmes in Australia and maintenance of productivity throughout this time depends heavily on maintaining a rate of collection that does not exceed two ejaculates per day (Cameron 1987).

By contrast with AI, in natural mating it is impossible to control the number of ejaculates per day which may vary between six and 40 or more per ram with the result that the size of individual ejaculates and the longer-term output of spermatozoa are both adversely affected (Cameron et al. 1984). In some cases the size of the ejaculate may be insufficient to provide an optimal dose in a single service and more than one service per ewe may be necessary to ensure normal fertility (Synnott et al. 1981). Fulkerson et al. (1982) showed that doses of spermatozoa less than 60×10^6 impaired fertility in natural mating (Fig. 7) and in some heavily worked rams Synnott et al. (1981) found that individual ejaculates sometimes fell as low as 10 x

10^6 spermatozoa. However, Cameron et al. (1987), using well-husbanded rams under field conditions, showed that individual ejaculates did not descend below 160 x 10^6 spermatozoa - ample to produce normal fertility.

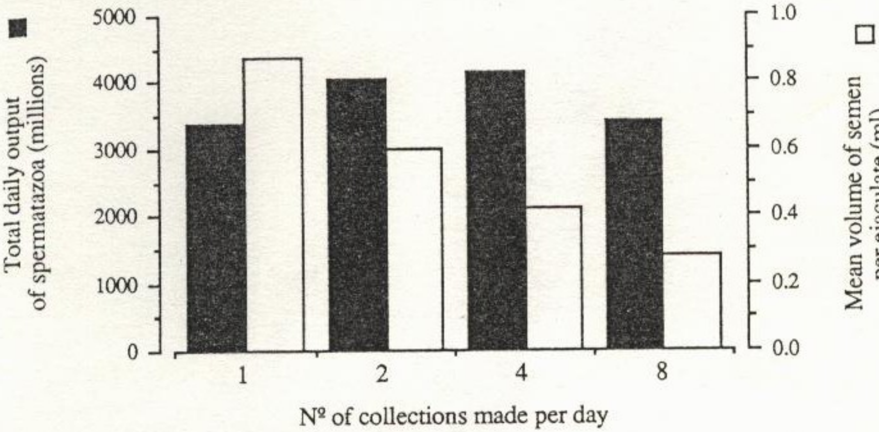

Figure 6 The output of spermatozoa per day and mean volume of individual ejaculates from rams from which semen was collected 1, 2, 4 or 8 times per day.

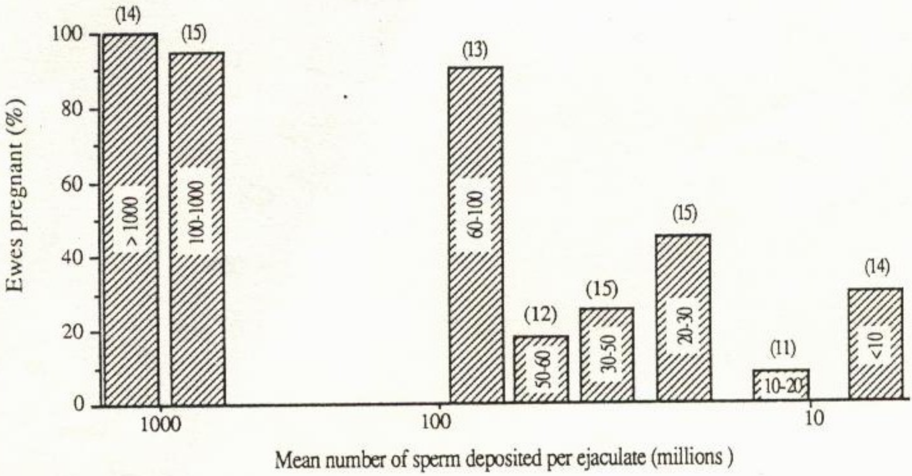

Figure 7 Percentage of ewes pregnant in relation to the estimated number of sperm received from a single ejaculate. (numbers of ewes in parenthesis) (From Fulkerson et al. 1982)

In the long term, naturally mating rams lose spermatogenic capacity because they lose testicular tissue during sustained mating activity, regardless of the season (Fig. 4; Lindsay et al. 1977).

It is interesting to note that the testicular volume falls rapidly during mating. Whether this dramatic fall in testicular volume is due to the mating *per se* or to the low intake of food by the rams during joining is uncertain. Knight et al. (1987) suggest that there could be a combined effect. Whatever the case, it is clear that rams during natural mating cannot be used for long periods of sustained activity without losing a substantial proportion of their capacity to produce spermatozoa.

This leads to a consideration of the minimum number of rams necessary in a naturally-mating flock to ensure good fertility. Since the daily output from a well-fed active ram can be from 4,,000 to 7,000 x 10^6 spermatozoa and only 60 x 10^6 spermatozoa are needed per ewe there is a theoretical case for using very low numbers of rams in naturally-mated flocks. In fact, Haughey (1959) and Allison (1975) have demonstrated that one ram per 300 ewes in the Romney Marsh breed in New Zealand is a feasible proportion that results in normal fertility. The problem in natural mating is that the distribution of semen by rams is by no means even. Rouger (1974), in France, and Tilbrook and Lindsay (1987) have shown that certain ewes are preferred by rams and that preferences are more or less consistent irrespective of the rams tested. This is reflected in the number of spermatozoa received during oestrus by the ewes (Fulkerson et al. 1982). Rams presented with eight ewes in oestrus simultaneously never mated with all eight ewes but mated many times with a few preferred ewes. Under field conditions where several rams are used, it seems that dominance of some of the rams over others ensures that subordinate rams are forced to consider the less attractive ewes and thus give them a chance of being fertilised (Synnott et al. 1981). In practical terms, under extensive conditions prevailing in Australia, Gherardi et al. (1980) and Fowler (1984) suggest that adequately prepared Merino rams with 400-500 g of testicular tissue each could be mated to a non-synchronised flock of ewes at the ratio of 1:100 without compromising the fertility of the flock.

THE EWE

Timing of breeding

Most sheep throughout the world are mated by natural insemination during the normal breeding season. Nonetheless, for reasons of management and economics, more and more use is being made of several techniques designed to induce ewes to conceive at precise times, often well outside the breeding season.

The sexual season under mid-latitudes starts when day length is decreasing and ends when day length is increasing but there is large variation between breeds (Hafez 1952; Thimonier et al. 1986). Thus the sexual season in Europe extends from the beginning of August to the end of January (Thimonier and Mauléon 1969) and in the Southern Hemisphere from February to July (Oldham 1980). However, the breeding season and the non-breeding season are not simple clear-cut entities. There are many important variations in the physiology of ewes that must be taken into account in order to effect successful controlled breeding. For example, the anoestrous period, which is simply the period when ewes are not receptive to rams, varies greatly in "depth" according to the time of the year, the breed of sheep, and the latitude in which they are observed. In all breeds the transition between the non-breeding and the breeding seasons is characterised by one or more "silent" ovulations in which the ovary is stimulated to ovulate but produces insufficient steroid hormones to prime and stimulate behavioural oestrus. This phenomenon is common at both the beginning and the end of the breeding season. During these periods the ewe is susceptible to stimulation by small quantities of exogenous hormones, and one of the techniques in controlling oestrus is to advance the onset of the breeding season by taking advantage of the ewe's sensitivity to manipulation at this period. In breeds like the Merino the "depth" of anoestrus is always relatively shallow and the amount of stimulation necessary to provoke breeding activity at any time of the non-breeding season is similar to that which is effective in other breeds only just before the beginning of the breeding season. A further factor that intervenes in the control of the timing of breeding activity is the phenomenon of lactational and/or post-partum anoestrus. It, too, varies in "depth" according to the length of the period since parturition and whether or not it coincides with the period of seasonal anoestrus.

Techniques used for controlling oestrus in ewes

(a) Progestagens plus PMSG

This technique, developed originally in Australia (Robinson 1965), is now used extensively in France and other European countries for controlling oestrus both within the breeding season and outside of it. The technique consists basically of establishing an artificial "corpus luteum" in each ewe and removing it simultaneously from all ewes so that cyclical activity begins synchronously. Usually the "corpus luteum" is in the form of a sponge impregnated with progestagen (commonly fluorogestone acetate) but also by subcutaneous implants which are removed at the appropriate time. PMSG is not strictly necessary at the time of sponge removal during the breeding season. It is obligatory in the non-breeding season but is used nevertheless in both the breeding and non-breeding seasons for two reasons. The first is that synchronisation of oestrus is more precise when PMSG is used, and the second is that a small dose of PMSG increases the ovulation rate and thereby increases overall fecundity.

Modern technology for the use of progestagens and PMSG in the control of oestrus as presently practised in France involves considerable "fine tuning". For example, when using fluorogestone acetate (FGA), 40 mg sponges are used for 12-14 days during the breeding season and 30 mg sponges for 10-12 days during the non-breeding season. This is because the hypothalamo-pituitary axis is more sensitive to the negative feedback of steroids during anoestrus than during the breeding season (Karsch et al. 1984). The dose of PMSG is adjusted according to a complex, but physiologically-based, matrix depending on the breed of ewe, the season of the year, the age of the ewe, and whether she is lactating or not. More recently attempts have been made to replace PMSG by the introduction of rams (Cognié et al. 1984). Results indicate that the success rate depends on breed, being high in breeds like the Merinos d'Arles, and the Caussenarde du Lot which do not have a deep anoestrus, and being relatively poor in breeds that have a deep anoestrus.

Standard techniques for out-of-season breeding require the ewe to become pregnant at the induced oestrus because she normally reverts back to anoestrus immediately after treatment. Attempts to devise a system to give non-pregnant ewes a second chance have had mixed results. Pearce et al. (1986) found reasonable success when they injected Merino ewes for a second time with PMSG on the 14th day after a standard progestagen-PMSG treatment (Table 1).

Table 1 Response to PMSG in ewes returning to oestrus after synchronisation and failure to become pregnant (from Pearce et al., 1986, and J Thimonier, unpublished)

	Proportion of ewes becoming pregnant in second cycle	Dose of PMSG	
		0 iu	**200 iu**
1a Australian Merino ewes	of the flock	108/325 (33%)	153/336 (46%)
	of non-pregnant ewes	108/193 (56%)	153/193 (79%)
		0 iu	**300 iu**
1b French crossbred ewes	of the flock	3/109 (3%)	7/108 (7%)
	of non-pregnant ewes	3/35 (9%)	7/35 (20%)

By contrast, in France, J Thimonier (unpublished data) had very little success in increasing the proportion of cross-bred ewes pregnant, using a similar technique. In this case the fertility at the first oestrus was very high (68%) but it is likely that the technique of using two injections is better suited to ewes with shallow anoestrus rather than ewes that have a deep anoestrus.

Another technique for dealing with the problem of dry ewes following induced, out-of-season breeding, is to divide the flock into two groups, pregnant and non-pregnant, and mate the non-pregnant ewes in the normal way at the beginning of the breeding season.

Management, both for the reproductive control of the flock and for the efficient use of feed, has been simplified in recent years by new techniques for pregnancy diagnosis, in out-of-season breeding, returns to oestrus are not a feasible criterion for non pregnancy but the progesterone test for non-pregnancy can distinguish those ewes without a corpus luteum of pregnancy at around day 19 (Thimonier et al. 1977). This test has now been largely superseded by real-time ultrasound scanning, or echography (Wilkins and Fowler 1984; Jardon et al. 1984). This method allows both the detection of pregnancy and an accurate estimate of the number of foetuses being carried from around day 35 of pregnancy. Newer refinements to the technique (J F Wilkins, unpublished data) using rectal rather than external probes allows the accurate detection of pregnancy from day 20 and the accurate prediction of the number of foetuses from day 25.

The ram effect

Transition from the non-breeding to the breeding season in ewes can be effected by at first isolating them, and then exposing them to the presence of rams or ram substitutes (castrate males treated with steroids, ewes treated with steroids, or even the smell of rams, particularly their fleeces). In ewes of breeds with shallow anoestrus this technique works at any time during the non-breeding season. In ewes of breeds characterised by deep anoestrus it is effective only during the four to six weeks before the onset of the breeding season.

It is clearly a natural phenomenon that may well be a mechanism for natural synchrony of wild species of sheep (Lindsay 1988) and has therefore been a component of the breeding of domestic genotypes of sheep, albeit mostly unknown to man, since domestication (Prud'hon and Denoy 1969). With a better understanding of the physiology of the ram effect that has emerged in the last decade (reviewed by Martin et al. 1986) its possibilities for the commercial management of flocks are only just being explored. Basically the stimulus from the male induces an accelerated pulsatile release of LH leading to a preovulatory surge, and ovulation about 48 hours after the stimulus. Normally this ovulation is not accompanied by oestrus but one cycle later (i.e. about 19 days after the initial stimulus) the ewe both ovulates and shows behavioural oestrus. One problem has been that an unpredictable number of ewes do not immediately produce an active corpus luteum following the first ovulation and therefore have a "short cycle" and re-ovulate (about six days later). This means that there is very poor synchrony of oestrus around day 19 because the ewes experiencing short cycles will not show behavioural oestrus for the first time until around day 25 after stimulus. An important practical finding was that a single injection of 20 mg progesterone given at the time that the ram stimulus was applied completely eliminates short cycles (Lindsay et al. 1982; Cognié et al. 1982). Now it is possible, using the ram effect and a single injection of progesterone, to obtain a high degree of synchrony between days 18 and 21 after the stimulus is applied. One large Australian sheep breeding cooperative that inseminates around 100,000 ewes per annum used this method for synchronising oestrus in over 20,000 sheep in 1986-87 and succeeded overall in inseminating 68-77 per cent of all ewes within five days (Table 2).

Table 2 Results of large scale programmes for synchrony of ewes for AI using the "ram effect: during anoestrus (from C A Curnow, unpublished data)

Age of ewes	% of all ewes in flocks inseminated in programmes of 4 days	5 days	6 days
Mature ewes	68 (n=4993)	74 (n=9026)	72 (n=3021)
Maiden ewes (ca. 1.5 yrs)	77 (n=420)	69 (n=2723)	-

The method has the advantage of being inexpensive and easy to manage under extensive conditions. Its disadvantages are that synchrony is not as precise as with other methods because it relies on the second oestrus after induction of ovulation rather than the induced ovulation itself and variations in the cycle length in ewes increase the spread of the response. It also relies on ewes being in anoestrus but not in deep anoestrus. If some ewes are cycling, as often happens in Merino flocks in Australia, or if ewes are in deep anoestrus, as is found in many northern hemisphere breeds in the middle of the non-breeding season, there will be no response, or an imperfect response.

Nonetheless, this technique is being practised over a wide range of environments (Folch et al. 1985; Khaldi 1984; Poindron et al. 1980). The possibilities of incorporating the advantages of synchrony of mating and of lambing into management systems in which the ewes are mated naturally rather than by AI are now being explored. Results indicate that this is a feasible objective but the very high concentration of ewes in oestrus over a short period puts enormous pressure on the rams and, as shown in Figure 8, joining ratios as high as 6 per 100 may be necessary to ensure adequate coverage (JF Wilkins, IW Purvis, unpublished data).

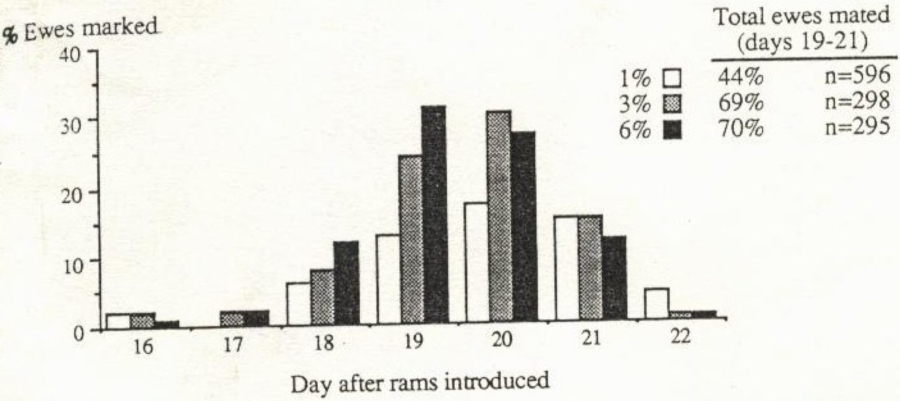

Figure 8 Distribution of mating in ewes induced to ovulate by the "ram effect" and 20 mg progesterone on day 0, mated to 1, 3 or 6% rams from days 16 to 22 after treatment (J F Wilkins and I W Purvis, unpublished data)

Treatment with melatonin

The photoperiodic message that stimulates ewes to enter or leave the breeding season is transmitted to the pineal gland. This gland converts the neural input into an hormonal signal which takes the form of a circadian rhythm of secretion of melatonin. The reproductive response is therefore determined by the melatonin pattern itself (Karsch 1984). The possibility of using melatonin to advance the breeding season has been extensively studied, particularly in Australia (Kennaway et al. 1982) and has led to the release in 1987 of a synthetically-made melatonin (Regulin [Gene Link Australia Limited]; Croker et al. 1987).

Reproductive activity cannot be maintained over very long periods under constant photoperiod regardless of its ratio of dark to light (Ducker et al. 1973). Alternating between long days and short days is considered to be the key to achieving control of sexual activity because long days appear necessary to restore the inductive effect of short days. As a result, treatment with melatonin, whether by ingestion, injection, or implant, induces reproductive activity efficiently only when the animals have been primed with long days. This occurs naturally at the end of spring or beginning of summer. At this time it is then possible to advance the onset of the breeding season (Arendt 1986) or to reduce the variability of the response to the ram effect (Chemineau et al. 1988). Under these conditions Kennaway et al. (1987) were able to advance the breeding season in a number of breeds in Australia (Merinos, Border Leicester, Dorset Horn, and crossbred). In addition this method is very promising for the efficient autumn mating of ewe lambs born in winter or early spring. However, if the melatonin treatment is applied too early in spring before the ewes have been "primed" by long days, then melatonin treatment has no effect on advancing the breeding season. As with most aspects of controlled breeding, variation among breeds, seasons, and physiological state, may well determine the success of melatonin treatments and the optimum regimes for combinations of these factors have yet to be worked out.

An important practical possibility for the more efficient use of melatonin has been suggested by Chemineau et al. (1988). These authors showed that, in goats, animals have to be primed by artificially long days for two to three months during winter, after which they respond strongly to melatonin and establish ovulatory cyclicity and maximum expression of oestrous behaviour during normal anoestrus. Long-day treatments were ineffective in inducing oestrous activity without the subsequent treatment with melatonin. So far this work has not been repeated in the ewe but experiments are now being undertaken (P Chemineau and J Thimonier, unpublished data).

Frequency of breeding

As new and successful techniques for out-of-season breeding and for breeding during lactation have become available, the possibility of breeding sheep more frequently than once a year, in a manner paralleling that of modern pig husbandry has been envisaged. Several attempts have been made to develop a commercial system of rapid turnover of pregnancies but attempts at ultra-rapid turnover have been universally disappointing and, at best, short-lived. One of the most comprehensive of these studies was that done on the experimental flock at Nouzilly and described by Thimonier et Cognié (1977). The ability of ewes to sustain a regime of frequent pregnancies appears to be limited and results eventually in the presence of too many dry ewes within the breeding system to be acceptable. The most frequent sustainable management system is probably one in which there are three lambings every two years (Tempest 1983; Robinson et al. 1977). Even in this sort of system a number of the lambings will be of ewes that failed to conceive in the previous round. For example, ewes that failed to conceive during an artificially induced oestrus in the non-breeding season may be successfully re-mated during the next round which would be in the breeding season.

The introduction of new technology into commercial sheep farming has been cautious but significant and is likely to continue to increase as techniques become more refined and more reliable. Jardon and Berny (1985) in a large-scale survey of sheep-meat flocks in France showed that intravaginal sponges are now used in 33% of flocks as part of their reproductive management. Of these only 9% confine their breeding to the autumn. By contrast, 78% used the technique to attempt to induce an extra gestation from ewes after lambing in the spring. The survey showed that there was little increase in lambs reared per 100 ewes in this case (119% to 122%) but farmers who used synchronisation techniques in an intensive system involving several lambing periods each year increased their productivity to 149%. Thus, a system has evolved over the last two decades in which each breeder has found a system of production which he believes "fits" his breed, the annual supply of feed, the management of the flock, and the markets. Combinations of light treatments, hormonal control, and artificial insemination for the out-of-season component in intensive systems are being proposed and tested with moderate experimental success (Ainsworth et al. 1985). Their introduction into commercial practice will be gradual and confined to those situations where the economics of the sheep industry warrant the relatively heavy investment necessary to set them up. Nevertheless, we can expect, in the next decade, to find even heavier commitment by the sheep industry to the use of management systems that take advantage of our increasing understanding of the physiology of reproduction in sheep.

REFERENCES

Ainsworth, L., Fiser, P.S., Heaney, D.P., Langford, G.A. and Shreska, J.N.B., 1985. Intensive husbandry of fecund sheep. In "Genetics of Reproduction in Sheep. (Ed. R.B. Land and D. Robertson). (Butterworths, London), pp. 399-409.

Allison, A.J., 1975. Flock mating in sheep. I. Effect of number of ewes joined per ram on mating behaviour and fertility. NZ J. Agric. Res. 18, 1-8.

Arendt, J., 1986. Role of the pineal gland in seasonal reproductive function in mammals. Oxford Rev. reprod. Biol. 8. Clarendon Press, Oxford. pp. 266-320.

Cameron, A.W.N., 1987. The production of spermatozoa by rams and its consequences for flock fertility. PhD Thesis, University of Western Australia.

Cameron, A.W.N., Fairnie, I.J. and Keogh, E.J., 1984. Semen quality, quantity and flock fertility. In "Reproduction in Sheep" (Ed. D.R. Lindsay and D.T. Pearce). (Australian Academy of Science, Canberra). pp. 79-85.

Cameron, A.W.N., Tilbrook, A.J., Lindsay, D.R., Fairnie, I.J. and Keogh, E.J., 1987. The number of spermatozoa required by naturally mated ewes and the ability of rams to meet their requirements. Anim. Reprod. Sci. 13, 105-115.

Chemineau, P., Pelletier, J., Guérin, Y., Colas, G., Ravault, J.P., Touré, G., Almeida, G., Thimonier, J. and Ortavant, R., 1988. Photoperiodic and melatonin treatments for the control of seasonal reproduction in sheep and goats. Reprod. Nutr. Develop. (in press).

Cognié, Y., Gray, S.J., Lindsay, D.R., Oldham, C.M., Pearce, D.T. and Signoret, J.P., 1982. A new approach to controlled breeding in sheep using the "ram effect". Animal Production in Australia. 14, 519-22.

Cognié, Y., Schinck, A., Martinet, J., Poulin, N. and Mirman, B., 1984. Activité reproductrice et maîtrise de l'ovulation chez la brebis. 9e Journées de la Rech. Ovine et Caprine ITOVIC-SPEOC, Paris. pp. 109-133.

Colas, G., Guérin, Y., Briois, M. and Ortavant, R., 1987. Photoperiodic control of testicular growth in the ram lamb. Anim. Reprod. Sci. 13, 255-262.

Colas, G., Guérin, Y., Clanet, V. and Solari, A. 1985. Influence de la durée d'éclairement sur la production et la fécondance des spermatozoides chez le bélier adulte Ile-de-France. Reprod. Nutr. Develop. 25, 101-111.

Croker, K., Dunstan, E., Reeve, J., Williams, A., McPhee, S., Ayton, B., Wagg, M., Pollard, T., Parker, J., Foote, M., Ritar, A. and Staples, L., 1987. Field studies of the use of melatonin implants to improve lambing percentages in spring joined Merino and crossbred ewes. (Abstr.) Proc. Aust. Soc. Reprod. Biol. 19, 21.

Dacheux, J.L., Pisselet, C., Blanc, M.R., Hochereau de Reviers, M.T. and Courot, M., 1981. Seasonal variations in rete testis fluid secretion and sperm production in different breeds of ram. J. Reprod. Fert. 61, 363-371.

Ducker, M.J., Bowman, J.C. and Temple, A., 1973. The effect of constant photoperiod on the expression of oestrus in the ewe. J. Reprod. Fert. Suppl. 19, 143-150.

Folch, J., Cognie, Y. and Signoret, J. P., 1985. Use of the :ram effect" for manipulation of the timing of onset and establishment of regular cycles and pregnancy in the ewe. Proc. 36th Meeting, European Assoc. Anim. Prod. - Kallithea, Greece. Ser. 1-3., pp. 122-123.

Fowler, D.G., 1984. Reproductive behaviour of rams. In "Reproduction in Sheep" (Ed. D.R. Lindsay and D.T. Pearce). (Australian Academy of Science, Canberra). pp. 39-46.

Fulkerson, W.J., Synnott, Anthea L. and Lindsay, D.R., 1982. Numbers of spermatozoa required to effect a normal rate of conception in naturally mated Merino ewes. J. Reprod. Fert. 66, 129-132.

Gherardi, P.B., Lindsay, D.R. and Oldham, C.M., 1980. Testicle size in rams and flock fertility. Proc. Aust. Soc. Anim. Prod. 13, 48-50.

Hafez, E.S.E., 1952. Studies on the breeding season and reproduction in the ewe. III. The breeding season and artificial light. J. Agric. Sci. 42, 232-233.

Haughey, K.G., 1959. Preliminary report on a tupping survey. Ashburton County. NZ Sheepfmg. Annu. 17, 17-26.

Jardon, C. and Berny, F, 1985. Reproduction, Enquête Nationale. Pâtre 320, 14-18.

Jardon, C., Montigny, G., André, D., Corteel, J.M., Baril, G., Cognié, Y., Botero, O. and Humbolt, P., 1984. Les methods de diagnostic de gestation applicable aux ovines et aux caprins. 8e. Journées de la Rech. Ovine et Caprine INRA ITOVIC, Paris. pp. 452-473.

Karsch, F.J., 1984. Endocrine and environmental control of oestrous cyclicity in sheep. In "Reproduction in Sheep" (Ed. D.R. Lindsay and D.T. Pearce). (Australian Academy of Science, Canberra). pp. 10-15.

Karsch, F.J., Bittman, E.L., Foster, D.L., Goodman, R.L., Legan, S.J. and Robinson, J.E., 1984. Neuroendocrine basis of seasonal reproduction. Recent Prog. Horm. Res. 40, 185-225.

Kennaway, D.J., Gilmore, T.A. and Seamark, R.F., 1982. Effect of melatonin feeding on serum prolactin and gonadotrophin levels and the onset of seasonal oestrus cyclicity in sheep. Endocrinology. 110, 1766-1772.

Khaldi, G., 1984. Variations saisonnière de l'activité ovarienne, du comportement d'oestrus et de la durée de l'anoestrus post-partum des femelles ovines de la race Barbarine: influences de niveau alimentaire et de la présence du mâle. Thèse Doct. Mention Sciences, Université des Sciences et Techniques du Languedoc, Montpellier. 168 pp.

Killeen, I.D. and Caffery, G.J., 1982. Uterine insemination of ewes with the aid of a laparoscope. Aust. vet. J. 59, 95.

Knight, T.W., Gherardi, S. and Lindsay, D.R., 1987. Effects of sexual stimulation on testicular size in the ram. Anim. Reprod. Sci. 13, 105-115.

Lindsay, D.R., 1988. Reproductive behaviour in survival: a comparison between wild and domestic sheep. Aust. J. Biol. Sci. (in press).

Lindsay, D.R., Cognié, Y. and Signoret, J.P., 1982. Méthode simplifiée de maîtrise de l'oestrus chez la brebis. Ann. Zootech. 31, 77-82.

Lindsay, D.R. and Ellsmore, J., 1967. The effect of breed, season and competition on mating behaviour of rams. Aust. J. Exp. Agric. Anim. Husb. 8, 649-652.

Lindsay, D.R., Gherardi, P.B. and Oldham, C.M., 1977. The effect of feeding a high protein supplement before joining on testicular volume in rams. In "Sheep Breeding". (Ed. G.J. Tomes, D.E. Robertson and R.J. Lightfoot). (WAIT Press, Perth). pp. 294-298.

Martin, G.B., Oldham, C.M., Cognié, Y. and Pearce, D.T., 1986. The physiological responses of anovulatory ewes to the introduction of rams - a review. Livestock Prod. Sci. 113, 219-247.

Masters, D.G. and Fels, H.E., 1984. Seasonal changes in testicular size of grazing rams. Animal Production in Australia 15, 444-447.

Maxwell, W.M.C., 1986. Artificial insemination of ewes with frozen-thawed semen at a synchronised oestrus. 2. Effect of dose of spermatozoa and site of intrauterine insemination on fertility. Anim. Reprod. Sci. 10, 309-316.

Moule, G.R., Braden, A.W.H. and Mattner, P.E., 1966. Effects of season, nutrition and hormone treatment on the fructose content of ram semen. Aust. J. Agric. Res. 17, 923-931.

Oldham, C.M. 1980. A study of sexual and ovarian activity in Merino sheep. PhD Thesis, University of Western Australia.

Oldham, C.M., Adams, N.R., Gherardi, P.B., Lindsay, D.R. and Mackintosh, J.B., 1978. The influence of level of feed intake on sperm-producing capacity of testicular tissue in the ram. Aust. J. Agric. Res. 29, 173-179.

Ortavant, R., 1958. Le cycle spermatogénétique chez le bélier. Thése Doct. es Sci. Nat., Université Paris.

Ortavant, R., Bocquier, F., Pelletier, J., Ravault, J.P., Thimonier, J. and Vollant-Nail, P., 1988. Seasonality of reproduction in sheep and its control by photoperiod. Aust. J. Biol. Sci. (in press).

Pearce, D.T., Oldham, C.M. and Gray, S.J. 1986. Progestagens, PMSG and the "ram effect" after artificial insemination in spring to synchronize non-pregnant ewes. Anim. Reprod. Sci. 10, 117-123.

Pelletier, J., 1971. Influence du photopériodisme et des androgènes sur la synthèse et la libération de LH chez le bélier. Thése Doct. es Sci. Nat., Université Paris.

Pelletier, J. and Almeida, G., 1987. Short light cycles induce persistent reproductive activity in Ile-de-France rams. J. Reprod. Fert. Suppl. 34, 215-226.

Pelletier, J., Brieu, V., Chesneau, D., Pisselet, C. and de Reviers, M., 1985. Abolition partielle des variations saisonnières du poids testiculaire chez le bélier par diminution de la période du cycle lumineux. C.r. Hebd. Séanc. Acad. Sci., Paris, 301, Sér. III. pp. 665-668.

Pelletier, J. and Thimonier, J., 1987. The measurement of daylength in the Ile-de-France ram. J. Reprod. Fert. 81, 181-186.

Poindron, P., Cognié, Y., Gayerie, F., Orgeur, P., Oldham, C.M. and Ravault, J.P., 1980. Changes in gonadotrophins and prolactin levels in isolated (seasonally or lactationally) anovular ewes associated with ovulation caused by the introduction of rams. Physiol. Behav. 25, 227-236.

Prud'hon, M. and Denoy, I., 1969. Effets de l'introduction de béliers vasectomisés dans un troupeau Mérinos d'Arles quinze jours avant le début de la lutte printemps sur l'apparition des oestrus, la fréquence des erreurs de détection des ruts et la fertilité des brebis. Ann. Zootech. 111, 95-108.

Robinson, T.J., 1965. Use of progestagen-impregnated sponges inserted intravaginally or subcutaneously for the control of the oestrous cycle in sheep. Nature, London 206, 39-41.

Robinson, J.J., Fraser, C. and McHattie, I., 1977. Development of systems of lambing sheep more frequently than once per year. In "Sheep Nutrition and Management". (US Feed Grains Council, London). pp. 5-33.

Rouger, Y., 1974. Etude des interactions de l'environment et des hormones sexuelles dans la régulation du comportement sexuel des Bovidae. Thèse Doct. es Sci. Nat., Université de Rennes.

Synnott, Anthea L., Fulkerson, W.J. and Lindsay, D.R., 1981. Sperm output by rams and distribution amongst ewes under conditions of continual mating. J. Reprod. Fert. 61, 355-361.

Tempest W.M., 1983. Management of the frequent lambing flock. In "Sheep Production". (Ed. W. Haresign). (Butterworths, London). pp. 467-481.

Thimonier, J., Bosc, M., Djiane, J., Martal, J. and Terqui, M., 1977. Hormonal diagnosis of pregnancy and number of foetuses in sheep and goats. In "Management of Reproduction in Sheep and Goats". Proc. Symp., University of Wisconsin, Madison, USA. pp. 79-88.

Thimonier, J. and Cognié, Y., 1977. Application of control of reproduction of sheep in France. In "Management of Reproduction in Sheep and Goats". Proc. Symp., University of Wisconsin, Madison, USA. pp. 109-118.

Thimonier, J. and Mauléon, P., 1969. Variations saisonnières du comportement d'oestrus et des activités ovarienne et hypophysaire chez les Ovins. Ann. Biol. anim. Biol. Biophys. 9, 233-250.

Thimonier, J., Terqui, M. and Chemineau, P., 1986. Conduite de la reproduction des petits ruminants dans les differentes parties du monde. In "Nuclear and Related Techniques in Animal Production and Health" (March 1986). IAEA, Vienna. pp. 135-147.

Tilbrook, A.J. and Lindsay, D.R., 1987. Differences in the sexual "attractiveness" of oestrous ewes to rams. Appl. Anim. Behav. Sci. 17, 129-138.

Wilkins, J.F. & Fowler, D.G. 1984. Ultasound imaging for litter size diagnosis in breeding flocks. In "Reproduction in Sheep" (Ed. D.R. Lindsay and D.T. Pearce). (Australian Academy of Science, Canberra). pp. 182-184.