J. Reprod. Fert., Suppl. **34** (1987), 187–199
Printed in Great Britain

Photoperiodic control of the onset of breeding activity and fecundity in ewes

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The seasonal nature of fertility of sheep has been accepted for many years (Hafez, 1952). It has also placed major restraints on farmers wishing to maximize farm output. Because sheep have a 5-month pregnancy and a 3-month lactation period it should be possible to produce 3 sets of lambs every 2 years. A major restraint on such a programme is the very strong seasonal photoperiodic influence upon fertility. In the farming systems of Europe there is a need to maximize the efficiency of labour-intensive management while in Australia there is a need to minimize labour-extensive farming systems. Both management strategies require better control of the onset of breeding activity. In many areas of Australia the late autumn start of breeding of Suffolk, Romney, Border Leicester and Perindale ewes means that the lambs are often weaned at a time of deteriorating pasture quality in late spring/summer with subsequent poor weight gain. An earlier season would allow better growth of the lambs before the summer burn off.

This review covers recent studies on the photoperiodic control of reproduction in ewes. We concentrate on evidence for the role of light, the pineal gland and melatonin on seasonal breeding in the ewe and discuss the ways this information has been used to gain control of sheep fertility and fecundity.

Role of daylength in seasonal breeding

The first attempts to influence sheep breeding by manipulating daylength were performed by Yeates (1949). Ducker *et al.* (1970) showed that abrupt and gradual changes in daylength ranging from 18·5 h light to 4·5 h light per day resulted in earlier onset of oestrus (Table 1). These experiments were started around the time of the summer solstice. Ducker *et al.* (1970) suggested and later confirmed experimentally that the interval to first oestrus provoked by short daylength was longer when ewes were treated in spring compared to summer (Ducker & Bowman, 1970a). These same authors provided compelling evidence that long daylength terminates the breeding season of ewes (Ducker & Bowman, 1970b). Using this basic information it has been possible to devise practical (expensive) treatment regimens involving daylength manipulation (often supplemented with hormonal treatment) which allow 8-month breeding cycles (Ducker & Bowman, 1972; Vesely, 1975).

Seasonal hormonal changes

The question of how seasonal changes in daylength result in the onset and offset of breeding activity has been addressed in many different ways. Walton *et al.* (1977) were amongst the first to describe in detail LH, FSH and prolactin concentrations during a year. The most striking seasonal hormonal change occurred in plasma prolactin concentrations; highest prolactin secretion coincided with periods of long daylength and lowest secretion coincided with short daylength. Studies involving

Table 1. Time interval from start of various shortened daylength treatments to onset of first oestrus in Clun Forest ewes (taken from Ducker *et al.*, 1970, and Ducker & Bowman, 1970b)

Treatment	Mean interval to oestrus (days)
Natural daylength	66·4 ± 7·4
3·75 h reduction	
Summer	59·5 ± 3·3
Spring	87·0 ± 7·0
7·75 h reduction	44·8 ± 2·7
11·75 h reduction	33·6 ± 3·3

artificial daylength changes and more frequent blood sampling reinforced the concept that shortening daylength results in lower prolactin concentrations and onset of ovarian activity (Walton *et al.*, 1980). Walton *et al.* (1980) suggested that the seasonally high prolactin concentrations may be responsible for the impaired ovarian function. The importance of prolactin changes in ewes is, however, controversial. Many studies have demonstrated low prolactin concentrations coincident with the onset of ovarian activity (Thimonier *et al.*, 1978; Kennaway *et al.*, 1983; Fig. 1), but there are also reports of ovarian activity in the presence of high prolactin values induced by photoperiod manipulation (Worthy *et al.*, 1985). The hypothesis of Walton *et al.* (1977) is especially attractive since hyperprolactinaemic humans invariably experience amenorrhoea (Bohnet *et al.*, 1976). McNeilly & Baird (1983) have shown that stimulation of prolactin concentrations by repeated TRH injections impaired ovarian oestradiol secretion in ewes. Therefore, while a discrete function for prolactin in the non-pregnant ewe is yet to be unequivocally proven, photoperiodically driven changes in basal prolactin secretion represent one of the most robust seasonal hormonal events.

The pineal gland has been shown to have a central role in the control of reproductive activity in rodents and a similar involvement is apparent in ruminants (Kennaway, 1984). The pineal hormone, melatonin, is secreted only during the night in sheep (Rollag & Niswender, 1976; Kennaway *et al.*, 1977). Early studies indicated that melatonin was present in pinealectomized ewes (Kennaway *et al.*, 1977), but when more specific antibodies were used in the RIA the unique pineal origin of melatonin in the sheep was confirmed (Kennaway *et al.*, 1982/1983). Extensive investigations by Rollag *et al.* (1978) and Kennaway *et al.* (1983) have shown that maximum melatonin values do not vary either through the oestrous cycle or the year. With respect to season, when an adequate blood sampling regimen is used, the only consistent change observed is a lengthening of the period of secretion of the hormone during the extended nights of winter. An appreciation of the importance of this observation will become apparent later in this review.

Effects of manipulation of photoperiod on reproductive parameters

Perturbation of physiological systems is a valuable tool for gaining an understanding of the role played by different endocrine organs. The role of daylength in the seasonal onset of oestrus in ewes became apparent in the experiments of Ducker *et al.* (1970). Similarly, the importance of the pineal gland became apparent when pinealectomized ewes were studied. If left in a normal environment, pinealectomized ewes continue to exhibit normal seasonal hormonal and fertility cycles (Roche *et al.*, 1970; Kennaway *et al.*, 1984). When pinealectomized ewes are challenged with an artificial change in daylength, however, the alternate inhibitory and stimulatory photoperiods are ignored; there is in fact a tendency for the ewes to maintain their previous seasonal breeding pattern.

One of the most instructive endocrine manipulations employed in the study of seasonal reproduction in the ewe has involved ovariectomy with oestradiol replacement using Silastic capsules

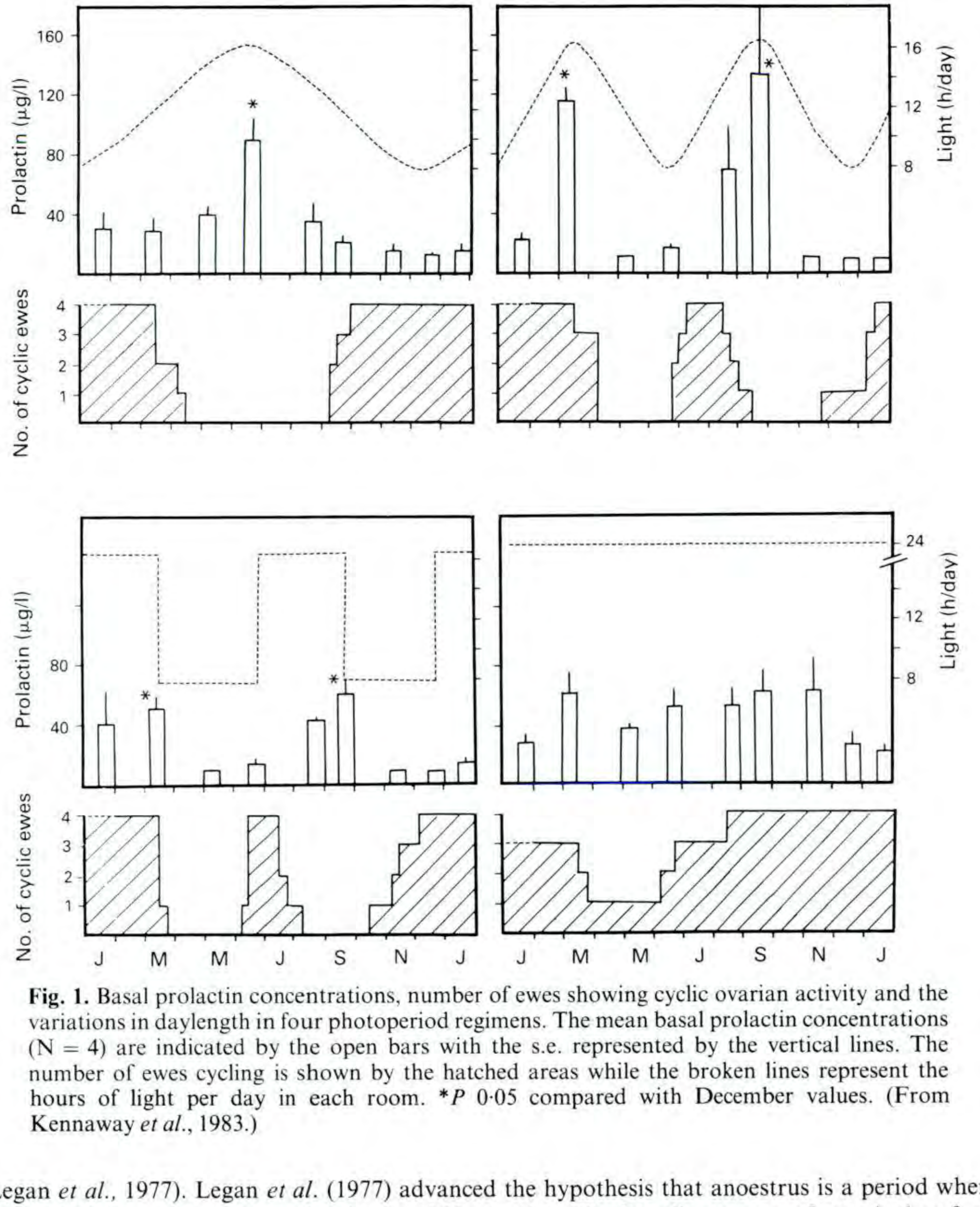

Fig. 1. Basal prolactin concentrations, number of ewes showing cyclic ovarian activity and the variations in daylength in four photoperiod regimens. The mean basal prolactin concentrations (N = 4) are indicated by the open bars with the s.e. represented by the vertical lines. The number of ewes cycling is shown by the hatched areas while the broken lines represent the hours of light per day in each room. *P 0·05 compared with December values. (From Kennaway *et al.*, 1983.)

(Legan *et al.*, 1977). Legan *et al.* (1977) advanced the hypothesis that anoestrus is a period when high sensitivity to oestrogen maintains low LH secretion. The breeding season of ewes is therefore characterized by lower oestradiol sensitivity at the hypothalamo/pituitary level and this permits the LH pulse frequency to increase during the periovulatory period, resulting in an LH surge and ovulation. Daylength is a major factor in the oestrogen sensitivity changes. If normal yearly swings in daylength are compressed into two 6-month periods there are 2 periods of breeding activity (Fig. 2) which is consistent with greater sensitivity to the negative feedback actions of oestrogen on LH secretion coincident with the periods of short daylength (Legan & Karsch, 1980; Fig. 3). Pineal involvement was implicated in studies of pinealectomized/ovariectomized/oestrogen-implanted ewes challenged with artificial daylength changes. Short-term pinealectomized ewes were unable to respond to the imposed daylengths with appropriate alterations in LH secretion (Bittman *et al.*, 1983; Fig. 3). Other studies have elegantly demonstrated that the duration of secretion of the pineal hormone melatonin is responsible for the changes in oestradiol feedback (Bittman *et al.*, 1983; Karsch *et al.*, 1984).

It was originally thought that ovariectomized ewes which were not treated with oestrogen had an unvarying LH pulse frequency during the year. Closer examination of these animals, however, indicated that the LH pulse frequency was lower during anoestrus than during the breeding season (Goodman *et al.*, 1982). This observation is described as a direct photoperiodic non-steroidal drive to the LHRH pulse-generating system. It is to be expected that this mechanism complements the steroidal feedback influences.

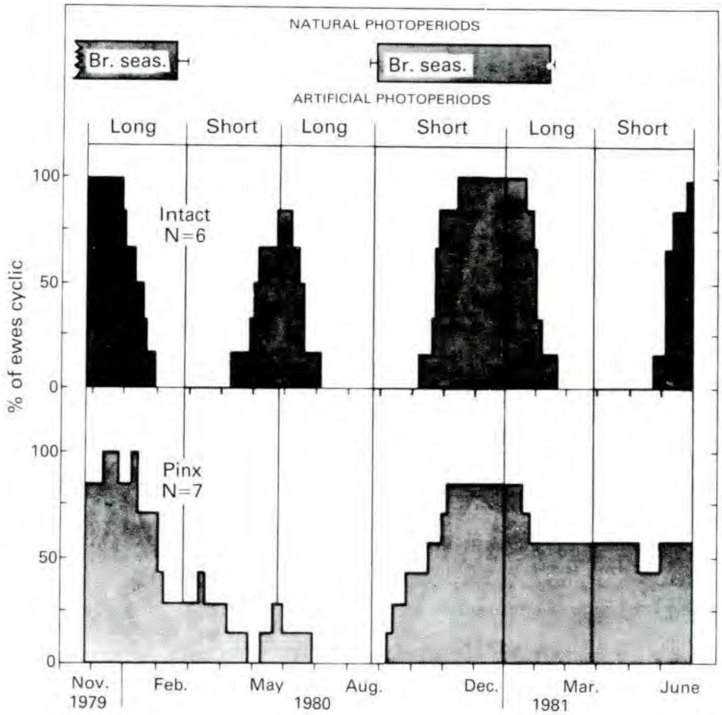

Fig. 2. Effects of artificial photoperiods on ovarian cyclicity in intact and pinealectomized (Pinx) ewes. Histograms indicate the percentage of ewes showing regular oestrous cycles. Photoperiodic treatments were 16 h light:8 h dark (long days) and 8 h light:16 h dark (short days). The normal breeding season was defined by 14 ewes maintained outdoors for 5 years. (From Bittman *et al.*, 1983.)

We have recently reported that long-term (>6 years) pinealectomized/ovariectomized/oestrogen-treated ewes maintained in the field with pineal-intact/ovary-intact ewes show no synchronized seasonal swing in LH secretion (Kennaway *et al.*, 1984). The LH concentrations were low, indicating high sensitivity to negative feedback. Pinealectomized/ovary-intact ewes, however, continued to show ovarian cyclicity in phase with pineal-intact ewes. We interpreted these results as indicating that the pineal drive to the oestrogen negative feedback system could be overridden by pheromonal influences of the other ewes and rams in the flock or by the so-called direct photoperiodic drive to the LHRH pulse generator. If the latter were true then the direct non-steroidal drive occurs through a non-pineal retino/hypothalamic projection.

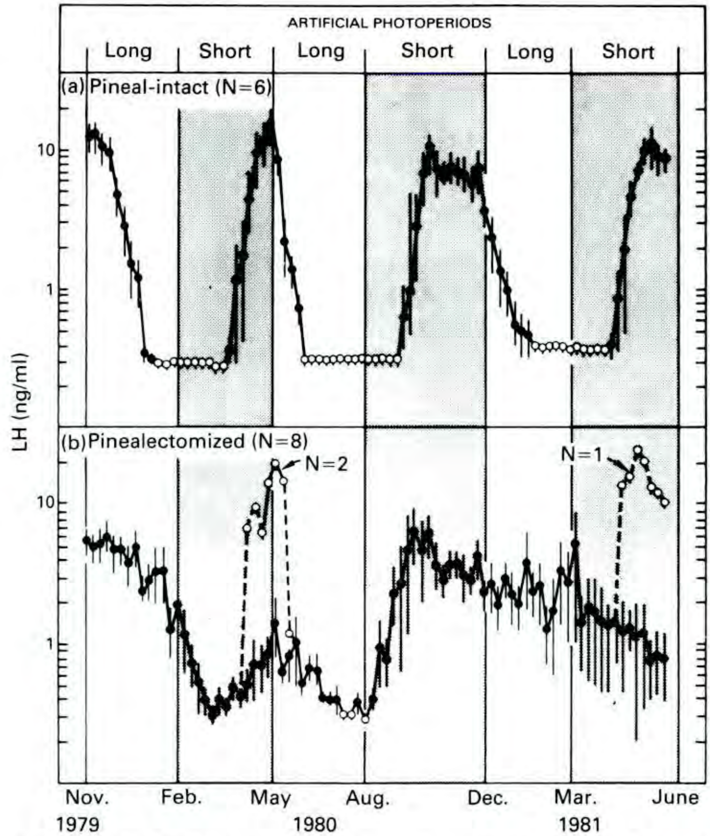

Fig. 3. Mean serum LH ($\pm$s.e.) in ovariectomized/oestradiol-implanted ewes. (a) Means of 2-weekly LH determinations in sham-pinealectomized ewes maintained in artificial photoperiod. (b) Alternating long (16L:8D) and short (8L:16D) daylength. (From Bittman *et al.*, 1983.)

Use of melatonin treatments to control the onset of breeding activity

Many groups have provided evidence supporting the role of light, the pineal gland and melatonin in the timing of the breeding season of ewes. While the mechanisms involved in the recognition by the hypothalamus of changes in duration of melatonin secretion are unknown, there is no doubt that appropriate administration of melatonin can alter the endocrine physiology of ewes.

In one of the first such experiments melatonin was chronically administered 8 h before darkness to anoestrous Border Leicester × Merino ewes maintained in long daylength (Kennaway *et al.*, 1982a). The melatonin was administered in food each day (when administered in this manner the melatonin is slowly absorbed and remains elevated for up to 8 h (Kennaway & Seamark, 1980)). The melatonin-treated ewes had an earlier onset of ovarian activity than did controls, with a lag time between the start of treatment and first oestrus of about 77 days, which is similar to the 'reaction time' observed in short daylength experiments. A decrease in prolactin concentrations after 30 days was a further indication that the treatment was mimicking the normal seasonal transition. Other groups have also confirmed the efficacy of melatonin in advancing the breeding season and promoting hormonal changes (Nett & Niswender, 1982; Arendt *et al.*, 1983; Howland *et al.*, 1984; Williams, 1984; Fig. 4).

More recently, continuous-release implants have been used in physiological studies and the hormonal changes observed are similar to those found after timed oral administration (Kennaway

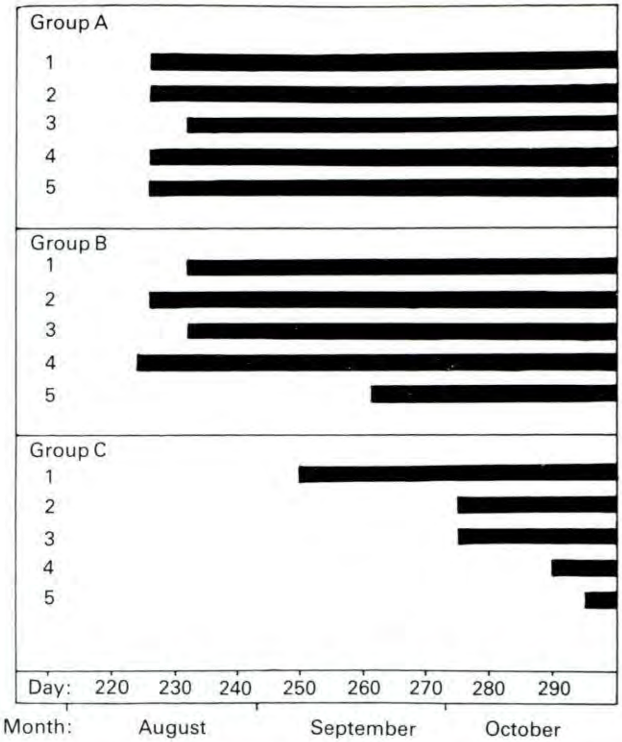

Fig. 4. Occurrence of oestrous cycles (solid bars) in 3 groups of 5 Suffolk cross ewes treated as follows. Group A: kept in 16 h light: 8 h darkness and fed 3 mg melatonin daily 8 h before darkness; Group B: kept in 8L:16D; Group C: kept in natural light. The experiment began on 15 June 1981. (From Arendt *et al.*, 1983.)

et al., 1982/1983, 1982b). When melatonin is continuously available during long daylengths, plasma prolactin concentrations are depressed within 14 days. Practical exploitation of this finding will be discussed below.

Use of light treatments and melatonin administration to gain control of fertility and fecundity

In this review much emphasis has been placed upon seasonal control of the onset of breeding activity and nothing about the quality of the fertility during the season. Clearly there are advantages in having control of when lambs are born and how many are born. The latter is normally genetically determined with some breeds being exceptionally fecund while in others twinning is rare. Seasonal influences upon fecundity in sheep have been recognized for many years (Land *et al.*, 1973; Scaramuzzi & Radford, 1983). Ovulation rate is highest in the late summer and autumn (the start of natural breeding activity) and declines progressively towards anoestrus. Hendy & Bowman (1974) have shown that ewes which had the earliest spontaneous ovulations had a higher ovulation rate than late breeding ewes of the same flock (Fig. 5). By the third cycle of the season, however, the ovulation rates were identical in early intermediate and late starters. Because daylength is the major environmental factor responsible for seasonality of sheep reproduction we have performed extensive studies on the effect of photoperiod on ovulation rate at first oestrus.

In the first such study, Dunstan (1977) showed that moving Border Leicester × Merino ewes into a darkened shed 4 h before sunset each day for 3–6 weeks in late spring, before the introduction of a ram, resulted in a 22–38% increase in lambs born. In subsequent studies we have shown that the

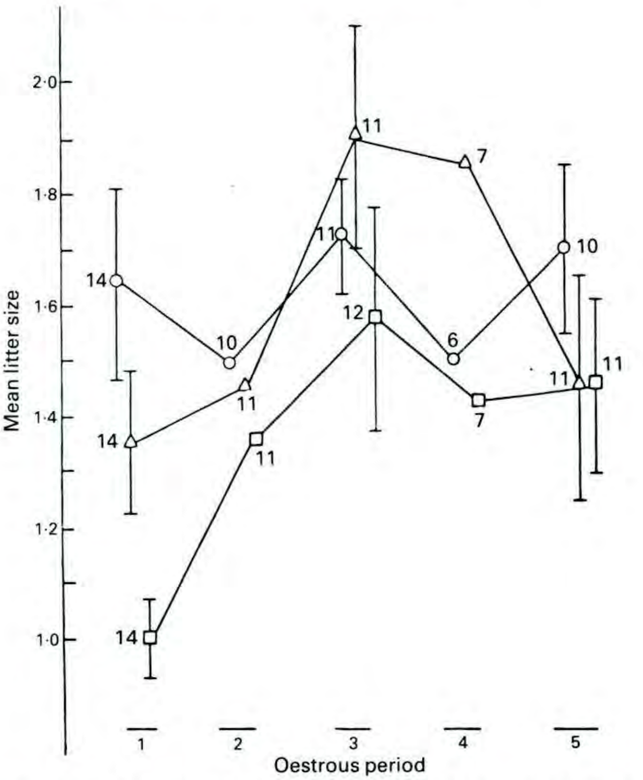

Fig. 5. Litter sizes in early (●), mid- (△) and late (□) mating phases in the first to fifth oestrous periods of the breeding season. Values are mean ± s.e. for the number of ewes indicated. (From Hendy & Bowman, 1974.)

artificial short daylength treatment can be successful if a vasectomized ram is used during the first 3 weeks and a fertile ram for the following 3 weeks (Figs 6 & 7; E. A. Dunstan, D. J. Kennaway & J. M. Obst, unpublished results). The advantage of delayed ram introduction, however, is a reasonably synchronized mating (21 days after introduction of rams) and a shorter lambing period, both being of practical importance. Most importantly, the phenomenon is highly reproducible; in one experiment on the same flock over a 6-year period a treatment involving 3 weeks short daylength, ram introduction and a further 6 weeks short daylength resulted in a mean 27% increase in lamb production each year (Fig. 8; E. A. Dunstan, D. J. Kennaway & J. M. Obst, unpublished results).

The hormone responsible for the short daylength-induced increases in fecundity was suspected to be melatonin because pinealectomized ewes had poor responses to the altered daylength regimen (Kennaway *et al.*, 1982/1983; E. A. Dunstan, D. J. Kennaway & J. M. Obst, unpublished results). When we compared a group of ewes on the short daylength treatment with ewes fed melatonin pellets (group-fed, average dose per ewe 2 mg) the number of lambs born was significantly increased in both groups (Fig. 9; D. J. Kennaway & E. A. Dunstan, unpublished results).

Further confirmation that melatonin was responsible for the response was obtained in trials on farms using much larger numbers of ewes. On 3 properties studied over 2 years, lamb production was increased by 10–20% using the 9-week treatment regimen. All the initial light and melatonin experiments had been performed on Border Leicester × Merino ewes in late anoestrus; under these conditions no effect on breeding season onset was observed because the rams induced early breeding in the control and treated animals. When melatonin was fed in January to a late breeding strain,

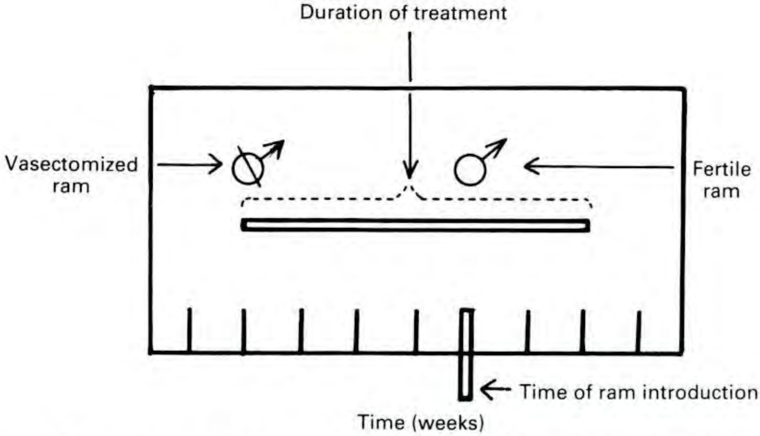

Fig. 6. Schematic representation of treatment designs used in short daylength, melatonin-feeding and melatonin-implant experiments with sheep (see Figs 7, 8, 9 and 12).

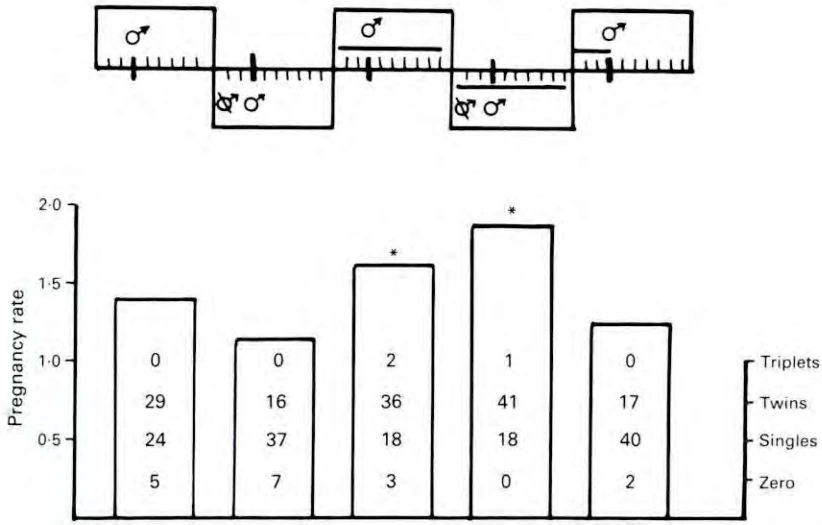

Fig. 7. Pregnancy rate (no. of lambs/ewe in group) in Border Leicester × Merino ewes given 4 h extra darkness each day for 3 weeks before fertile ram introduction (see Fig. 6 for treatment details). The actual numbers of singles, twins and triplets are also represented. The asterisk indicates the treatments resulting in significantly more lambs being born compared to the control groups ($P < 0·05$).

the Perindale (normal spontaneous ovarian activity and conceptions occur in March/April), we observed (a) an earlier onset of breeding activity in treated ewes versus control fed ewes in the same flock and (b) a 42% increase in lamb production (R. F. Seamark & D. J. Kennaway, unpublished results).

Daily light deprivation or melatonin feeding may not be very practical procedures for farm use except in intensive farming systems. We had, however, demonstrated hormonal effects (decreased prolactin concentrations) in ewes treated with Silastic envelopes of melatonin (Kennaway *et al.*, 1982/83) and proposed that continuous melatonin administration would result in earlier breeding and increased fecundity. The development of a continuous release/biodegradable formulation of

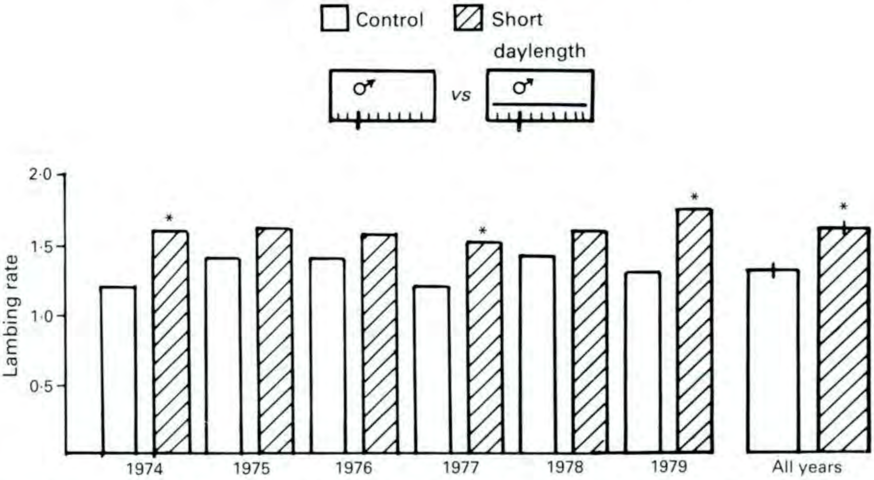

Fig. 8. Lambing rate (no. of lambs born/ewe in group) in Border Leicester × Merino ewes given 4 h extra darkness each day for 3 weeks before fertile ram introduction (see Fig. 6 for treatment details). The same flock was treated at the same time of the year for 6 years. The asterisks indicate the treatments resulting in significantly more lambs being born compared to the control groups in 3 of the 6 years ($P < 0{\cdot}05$). When analysed over the entire 6-year period the difference was also significant ($P < 0{\cdot}05$).

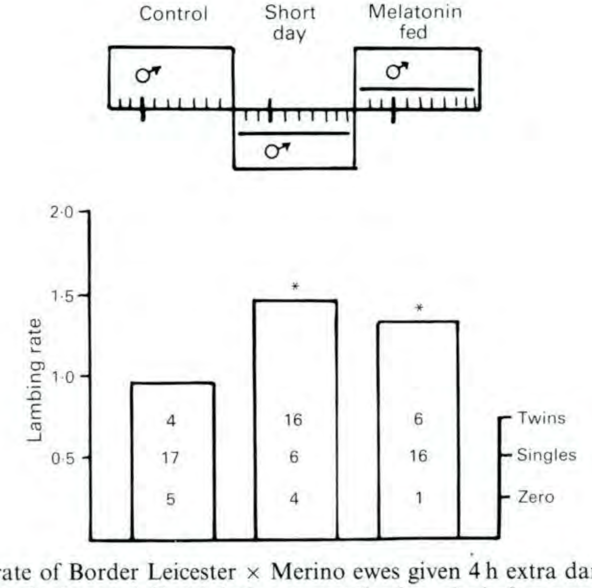

Fig. 9. Lambing rate of Border Leicester × Merino ewes given 4 h extra darkness each afternoon or fed melatonin (2 mg) daily 4 h before sunset for 3 weeks before ram introduction (see Fig. 6 for treatment details). Also shown are the actual numbers of single and twin lambs born.

melatonin by Gene Link (Australia) Pty Ltd in conjunction with the Institute of Drug Technology, Victoria, The Victorian Department of Agriculture and Rural Affairs and the University of Adelaide, has facilitated research in this area. When melatonin is continuously delivered to produce circulating concentrations of melatonin in excess of 1000 pmol/l the breeding season can be advanced and an increase in fecundity observed. Two experiments will be described which illustrate these effects.

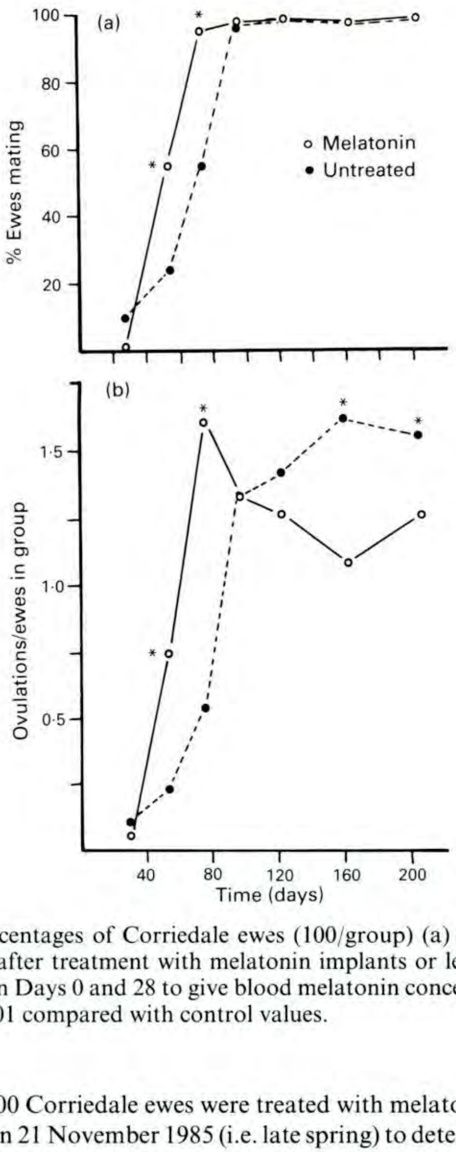

Fig. 10. Cumulative percentages of Corriedale ewes (100/group) (a) mating to vasectomized rams and (b) ovulating after treatment with melatonin implants or left untreated. Melatonin implants were inserted on Days 0 and 28 to give blood melatonin concentrations >1000 pmol/l for ~ 70 days. $^*P < 0.001$ compared with control values.

In the first experiment 200 Corriedale ewes were treated with melatonin implants or placebo on 24 October 1985 and again on 21 November 1985 (i.e. late spring) to determine whether the increased lamb production was due to increased ovulation rate or lower fetal wastage. Vasectomized harnessed rams were run with the ewes throughout the experiment and daily observations on oestrous activity were made. The ewes were subjected to endoscopy monthly to determine ovulation rates. Figure 10 shows that the melatonin implants caused a significant increase in the proportion of ewes ovulating at 53 and 74 days after the start of treatment. The treatment also significantly increased the number of ovulations per ewe ovulating on Days 53 and 74 and therefore increased the number of ovulations per ewe in the group (Fig. 10; L. D. Staples, A. Williams, S. McPhee & B. Ayton, unpublished results).

In the second experiment (L. D. Staples, S. McPhee, B. Ayton, J. Reeve & A. Williams, unpublished results) we tested the interrelationship between onset of breeding activity and increased pregnancy rate. We used 3 breeds of sheep, the Merino, Border Leicester × Merino, and Romney to represent 'non-seasonal', 'moderately seasonal' and 'highly seasonal' breeding patterns, respectively. The experiments were conducted such that the times of introduction of rams were conservatively 'early' for each breed, i.e. 8 November 1985, 18 November 1985 and 28 January

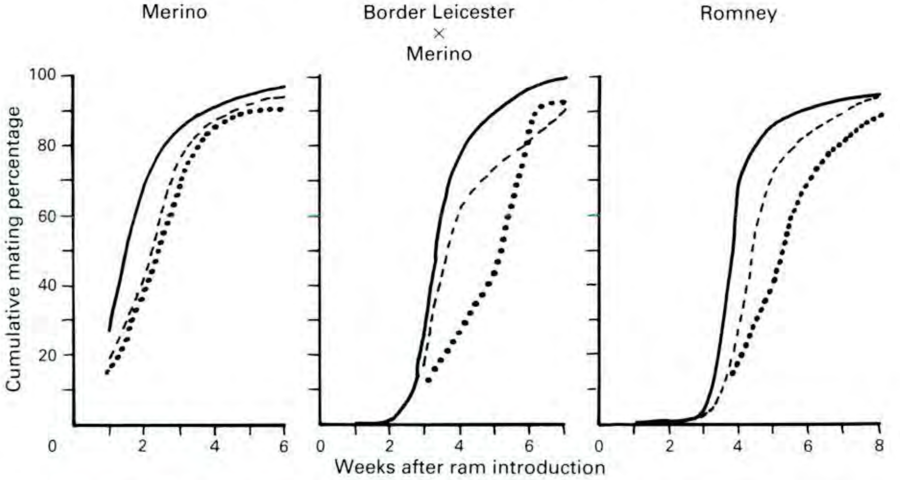

Fig. 11. Cumulative percentages of Merino, Border Leicester × Merino and Romney ewes mating to fertile rams after treatment with melatonin implants (——), left untreated but run with the melatonin group (– – –) or left untreated in an isolated part of the property (· · · · ·). Day 0 is the time of ram introduction.

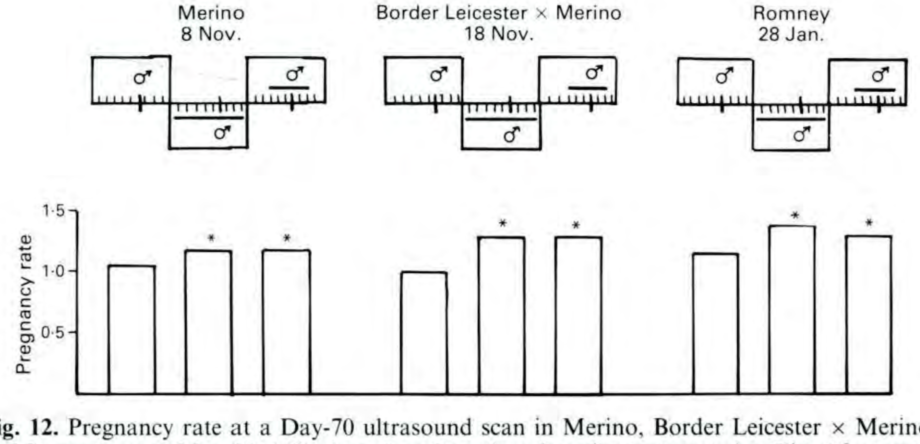

Fig. 12. Pregnancy rate at a Day-70 ultrasound scan in Merino, Border Leicester × Merino and Romney ewes (N = 93–140) given 5- or 9-week melatonin treatments (see Fig. 6 for treatment details). $*P < 0{\cdot}001$ compared to control group value.

1986 respectively. Two treatments were used: the first involved the insertion of melatonin implants 6 weeks before ram introduction and giving a 9-week melatonin coverage, and the second treatment involved melatonin treatment 3 weeks before ram introduction with a total of 5 weeks melatonin coverage. The melatonin- and placebo-implanted ewes were run as a single flock and a third untreated control group was maintained in an isolated part of the property. Figure 11 shows the cumulative mating profiles for the 6-week pretreatment groups only. There was no effect on breeding of Merinos because many ewes in the flock were already cyclic at the start of the experiment. However, the Border Leicester × Merino and Romney ewes began to breed earlier than did placebo-implanted controls and the separate control flock. In all three breeds both treatment regimens resulted in significant increases in the number of fetuses at a Day-70 ultrasound scan (Fig. 12).

The chronically elevated melatonin concentrations achieved after implantation of the Gene Link (Aust.) formulation promotes early oestrus in several breeds of sheep. Moreover, the phenomenon first reported by Hendy & Bowman (1974) (the higher litter size of ewes mating earliest in the season) is likely to be the result of photoperiodic influences and can be mimicked by light or melatonin treatments. The increased ovulation rate does not simply follow on from the early onset of oestrus, because control ewes run with melatonin-treated ewes breed early due to a 'ewe effect' but do not have a higher ovulation response compared to the separate control group.

Conclusions

The seasonal nature of sheep breeding has been tolerated for centuries and management practices have evolved to compensate for it. With the desire to maximize sheep production numerous procedures have been used to induce out-of-season breeding (e.g. progesterone treatment, GnRH injections) but all have failed to account for the persisting inhibitory photoperiodic signals the sheep were receiving during anoestrus. A significant advance in our understanding of seasonality has come with the recognition of the vital roles the pineal gland and its hormone melatonin play in relaying photoperiodic information to the endocrine system. The development of biologically active, biodegradable, continuous release formulations of melatonin should allow producers to gain almost complete control of the time their animals can conceive and maximize their lamb production. From an endocrinologist's viewpoint, however, there are still many questions to be answered concerning how melatonin acts at the neuroendocrine level to promote cyclic ovarian activity and maximize the number of ova shed by the ewes.

We thank R. Male, G. Gleeson, R. F. Seamark, A. Gilmore, P. Royles, F. Carbone, H. Webb, A. Williams, S. McPhee, J. Reeve and B. Ayton. Original work cited in this review was generously supported by grants from the Australian Meat Research Committee, the National Health and Medical Research Council and Gene Link (Aust.) Pty Ltd.

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