Seasonality of Reproduction in Sheep and its Control by Photoperiod*

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Abstract

Seasonality of the reproductive cycle in sheep is a general phenomenon for mid-latitude breeds. The proximal part (breeding season) and also partially distal part (end of gestation and beginning of lactation) of this cycle is controlled by photoperiod, whatever the form of light regimens. Data are presented which indicate that male and female do not necessarily have the same photoperiodic sensitivity. Gonadal stimulation in the ram starts 1·5–2 months earlier than in the ewe under annual variations. Photoperiod controls the reproductive cycle by the intermediary of the hypothalamo–pituitary axis. There are both a steroid-independent and a steroid-dependent effect of light, depending on both decreasing and increasing daylength in mid-latitudes.

Data are also presented which support Bunning's hypothesis on photoperiodic time measurement in mammals. Sheep measure photoperiodic time by using a circadian rhythm of photosensitivity. Daylength is not measured by the total duration of exposure to light but by the illumination of two special set points during the day, one of them entraining the circadian rhythm of photosensitivity and the other inducing or not inducing a physiological response if it is coincident, or not coincident, with photoinducible phase of that rhythm. A photoinducible phase has been found for prolactin secretion, and perhaps also for LH secretion.

Melatonin secretion is used by sheep for measuring daylength. However, that secretion disappears during two set points during the day, thus raising the possibility of using alternatively melatonin and light pulse for controlling the reproductive cycle in sheep.

Introduction

It is well-known that, in sheep, reproduction is seasonal, at least in breeds originating from temperate climates. Natural selection pressure has favoured propagation of those genes which couple the time of birth to the most appropriate phase of the annual cycles of climate and food availability, i.e. in early spring (Jewell *et al.* 1974; Ortavant *et al.* 1985; Short 1985). Reproductive seasonality is also found in some other farm species (goats, horses and cattle) when they have returned to the feral state (Ortavant *et al.* 1985).

Thus, natural selection has provided mammals, especially sheep, with signalling systems which couple some kinds of environmental variations with the appropriate neuroendocrine responses in order that sexual activity occurs at the most favourable season depending on the length of gestation. Photoperiod is the most noise-free annual predictor in the mammalian environment.

In the domestication of animals, man has tried to eliminate the unfavourable effects of environmental factors and has also practised artificial selection based on particular traits. Domestication has thus caused modifications of genetic characteristics of populations and

has induced considerable variability in the occurrence of breeding season within each domesticated species. Nevertheless physiological mechanisms underlying seasonality have been retained in spite of several thousand years of domestication.

In this paper concerning the seasonality of sheep reproduction and its control by photoperiod we will consider the reproductive cycle in its widest meaning, including not only the proximal part of this cycle, that is, the sexual season or breeding season, but also the distal part of the cycle, i.e. the end of gestation, parturition and suckling of the young.

Seasonality of the Reproductive Cycle in Sheep
Proximal Part: Breeding Period
Gonadal activity and sexual behaviour (Fig. 1)

Under mid-latitudes, seasonality is a general phenomenon. Generally, in ewes, the sexual season, i.e. ovulatory and/or oestrous activity, starts by mid- or the end of summer, that is during decreasing day length, and ends during winter, that is during an increasing one (Hafez 1952). Thus, in Ile-de-France ewes, the beginning of the sexual season is by mid-August and the cessation by the end of January (Thimonier and Mauléon 1969). However, there are large variations between breeds, with some breeds beginning their period of sexual activity close to the summer solstice and others after the autumn equinox (Walrave *et al.* 1975; Thimonier and Gauthier 1984). There are also variations between individuals within a breed, some ewes having only a small period of anoestrus (Thimonier and Mauléon 1969) or even none at all.
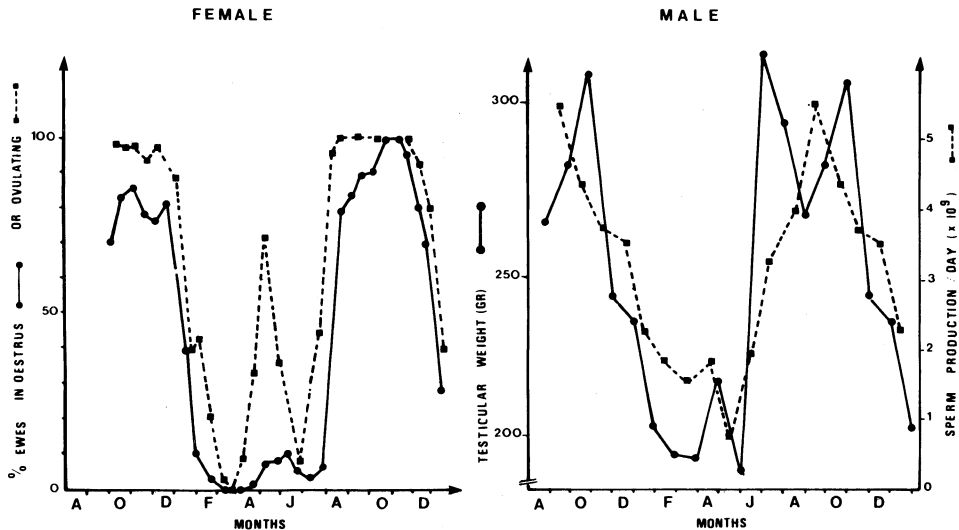

Fig. 1. Comparative sexual activity of female (left) and male (right) Ile-de-France sheep. The curve of ovulating ewes (■——■), determined by regular endoscopic observations of the ovaries, is parallel to that of the appearance of oestrous behaviour (●———●). Silent ovulations not related either to the end or the onset of the sexual season occur during mid-anoestrus (April–May). (Adapted from Thimonier and Mauléon 1969.) The daily sperm production (■——■) is minimal from February to May and maximal from August to October. (Adapted from Dacheux *et al.* 1981.) The testis weight (●———●) varies from 180–190 g in February–May to 300–320 g from July to October. (From Pelletier and Ortavant 1970.)

Both ovulatory activity and oestrus behaviour show parallel seasonal variations. However, there are some discrepancies at the beginning and at the end of the sexual season when some ovulations occur without oestrus. In some breeds, during anoestrus, silent ovulations not related either to the end of the preceding or to the onset of the subsequent sexual season are observed (Thimonier and Mauléon 1969; Land *et al.* 1973), i.e. during increasing daylength. Reardon and Robinson (1961) and Fletcher and Lindsay (1971) demonstrated a seasonal variation in the incidence of oestrus in progesterone-primed, spayed, oestradiol-treated ewes corresponding to the seasonal variations in the expression of oestrus behaviour in intact ewes. These seasonal

variations in sensitivity to oestrogen are, however, modulated by the nutritional status (Gibson and Robinson 1971).

The ovulation rate increases from the onset of the breeding season to the mid-breeding season, then decreases (Thériez et al. 1971; Ricordeau et al. 1978).

Seasonal variations of gonadal activity are not sex-limited, although they are less pronounced in the ram than in the ewe. The testis weight in the adult Ile-de-France ram varies from 180–190 g in the late winter–early spring to 300–320 g in late summer and autumn (Pelletier and Ortavant 1970). The increase in testis weight starts before the beginning of summer and its regression begins before winter in rams not trained for mating. The testis weight depends on spermatogenesis efficiency which varies according to the season: on average $8 \cdot 5 \times 10^6$ spermatozoa are produced per gram of testicular parenchyma in spring versus $12 \cdot 2 \times 10^6$ in autumn (Ortavant 1959). As a result, the daily sperm output appreciated by rete testis canulation (Dacheux et al. 1981) varies from 1×10^9 spermatozoa at the minimum in spring up to $4 \cdot 8 \times 10^9$ at the maximum in late summer.

Furthermore the quality of semen (indicated by the percentage of normal spermatozoa) and its fertility are lower in spring than in autumn as demonstrated by Colas (1979, 1980) using both spring and autumn deep-frozen semen for artificial insemination of synchronized ewes either in spring or in autumn.

Finally, the sexual behaviour of rams in 10-min standardized tests in pens is higher in summer and autumn than in winter or spring (Rouger 1974).

Similar tendencies have been observed in many other breeds even if there were variations between them or between individuals within a breed for the criteria cited above (Dacheux et al. 1981; Pelletier et al. 1981; Colas et al. 1984).

Gonadotrophic hormones

Male and female sexual activity depends on pituitary gonadotrophic function. In the Ile-de-France ewe, pituitary FSH and LH concentrations are twice as low during deep anoestrus as on day 12 of the oestrous cycle during the breeding season (Thimonier and Mauléon 1970). Similarly the pituitary LH concentration in rams of the same breed is twice as high from the end of June to the end of November as from December to May (Pelletier and Ortavant 1970), but the beginning of the increase occurs earlier than in the ewe. The seasonal variations in pituitary FSH concentration are less clear, two peaks being observed in rams, one in February and the second in July (Pelletier and Ortavant 1970).

The secretion profile of LH is pulsatile. In ewes, the LH pulse frequency is low in anoestrus and high during the sexual season. During the oestrous cycle, pulse number and amplitude are modulated by the levels of endogenous progesterone and oestradiol (review by Martin 1984). In Ile-de-France rams, LH pulse frequency is low (three pulses/24 h) by the beginning of winter and high (six pulses/24 h) as early as June (Pelletier et al. 1982). Each LH pulse induces a testosterone peak; thus the frequency of testosterone peaks increases with the frequency of LH pulses (Pelletier et al. 1982).

Studies on plasma FSH in the ram demonstrate a rise in the level from April to May with a maximum in August–September followed by a drop (Lincoln and Peet 1977; Sanford et al. 1978; Ravault et al. 1980; Kennaway et al. 1981). Results are rather conflicting for the ewe; according to various authors plasma FSH levels are said to stay constant, to be increased, or to be decreased during the breeding season (see Ortavant et al. 1985).

Distal Part: End of Gestation and Lactation

It has been shown that birth weights of twin lambs are higher during spring lambing than during autumn lambing, even if pregnant ewes received a large quantity of food (Tissier and Thériez 1979). However, Bosc et al. (1982) did not observe differences in birth weight of lambs between lambing in both seasons, but they did not separate twin from single lambs in their analysis.

There are, to our knowledge, no data concerning seasonal influence on milk production in the ewe because lambing of milked ewes generally occurs only in one season. However, such seasonal effects are known to exist in other species. In cattle, milk yield is higher after calving in spring than in other seasons (Decaen and Journet 1966) and in goats, Linzell (1973) observed seasonal oscillations in the rate of milk secretion.

Some hormones may be related to these seasonal variations; for example ovine placental lactogen (OPL) may be directly or indirectly related to lamb birth weight (Djiane and Kann 1975; Butler *et al.* 1981; Taylor *et al.* 1982) and prolactin is one of the essential hormones in mammogenesis and lactogenesis (Denamur 1971; Delouis *et al.* 1980). Bosc *et al.* (1982) did not find seasonal variations of plasma OPL levels, but most studies on seasonal variations in prolactin in farm mammals have shown a clear relationship between the level of this hormone and the seasons: plasma prolactin levels increase in the spring, reaching a maximum in summer, then declining to a minimum in winter in both males and females. This is true for sheep (ram: Ravault 1976; ewe: Thimonier *et al.* 1978; Yenikoye and Ravault 1981). There are no differences in this pattern between breeds (Webster and Haresign 1983).

Photoperiodic Control of the Reproductive Cycle in Sheep
Proximal Part: Breeding Period
Gonadal activity
Photoperiod is now considered as the main factor controlling the initiation of the ovine sexual season in both the female and the male, at least for those bred under mid-latitudes. Classical experiments clearly demonstrate the entrainment of gonadal activity by light (Fig. 2).

Thus, artificial reversal of the annual rhythm of photoperiodic variations induces reversal of the period of sexual activity measured by oestrus and/or ovulatory activity in the ewe (Yeates 1949; Thwaites 1965) and by recrudescence and regression of testicular size in the ram (Alberio and Colas 1976).

Under a 6-month light cycle which reproduces in 6 months the annual variations of daylength (Ortavant and Thibault 1956), ewes experienced two periods of sexual activity starting during the shortest daylengths and ending during the longest ones (Mauléon and Rougeot 1962). Similarly, rams submitted to such a rhythm of daylength variations demonstrated two periods of testicular growth and two periods of testicular regression per year. The increase starts when daylength is at its highest and ends when daylength is at its lowest (Lindsay *et al.* 1984), i.e. almost at the opposite phase of that recorded for ewes.
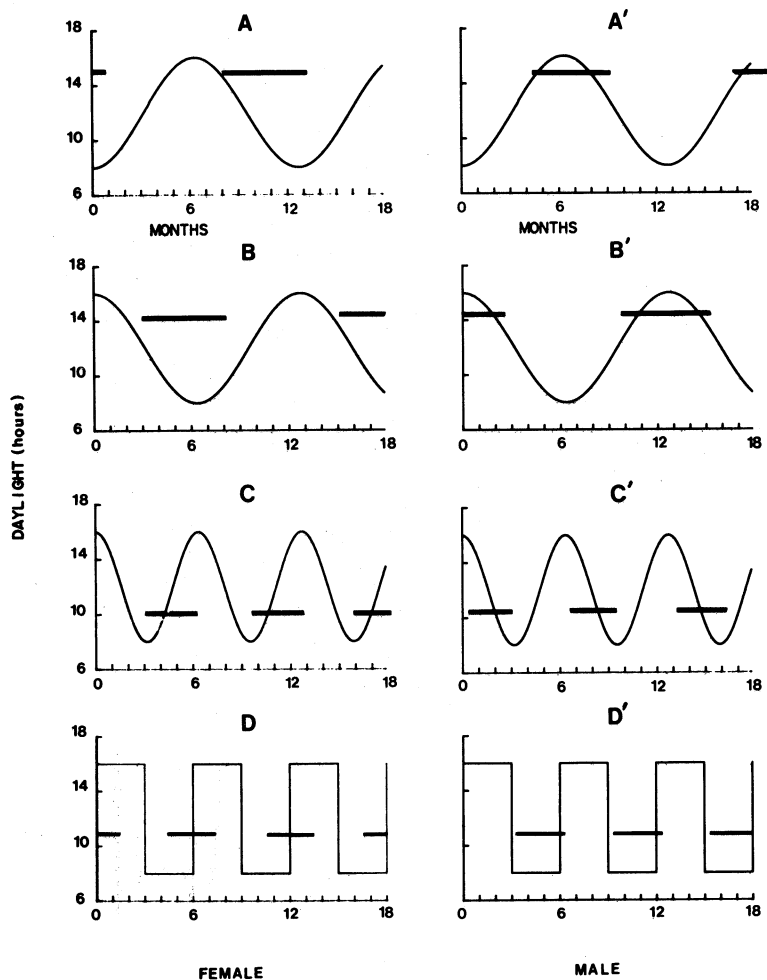
Finally, alternation of periods of constant long (16 L–8 D) and constant short (8 L–16 D) days induced alternation of sexual activity and inactivity both in the male (Lincoln and Davidson 1977) and in the female (Legan and Karsch 1980). Under alternations every 3 months, the period of ovulatory activity begins within 50 days after the shift from long to short days (Legan and Karsch 1980; Thimonier 1986). But testicular growth starts just after the shift between long and short days and ceases just after a shift between short and long days (D'Occhio *et al.* 1984).

Gonadotrophic activity
Under annual artificial light cycles gonadotrophic activity follows the same variations as under normal annual cycles (see above). Under 6-month light schedules in Ile-de-France and Préalpes du Sud rams, pituitary FSH and LH levels are much higher in short than in long days (Pelletier and Ortavant 1970). The frequency of plasma LH pulses is then the highest during decreasing daylengths, the stimulation being initiated during the longest days (Lindsay *et al.* 1984). Also a progressive decrease of daylength causes a rise in the release of plasma FSH and LH in rams (Schanbacher and Ford 1979).

Under alternation of constant long and short days, numbers of plasma FSH and LH pulses are higher in short days than in long days (Lincoln and Davidson 1977; Lincoln 1979). Gonadotrophins are found to increase a few days after the shift from long to short days (Lincoln and Peet 1977; D'Occhio *et al.* 1984). The appreciable increments in testosterone occurred

3-4 weeks only after the increase in plasma LH (D'Occhio *et al.* 1984). Ovariectomized ewes bearing an oestradiol implant also present a rise in plasma FSH and LH levels after the shift from long to short days but the increases do not occur until 1·5 months following the shift (Legan and Karsch 1980).

Fig. 2. Comparative gonadal activity of female (left) and male (right) sheep: adapted results from classical experiments demonstrating the entrainment of gonadal activity by light. — Period of oestrous or ovarian activity for the female; period of testicular growth for the male.

A: Thimonier and Mauléon (1969)   A': Pelletier and Ortavant (1970)
B: Thwaites (1965)   B': Alberio and Colas (1976)
C: Mauleon and Rougeot (1962)   C': Lindsay *et al.* (1984)
D: Thimonier (1986)   D': D'Occhio *et al.* (1984)
   Legan and Karsch (1980)

These experiments and observations in sheep demonstrate the strength of photoperiod for the entrainment of gonadal activity both in the female and the male and emphasize the difference between the two sexes: the male starts earlier than the female, approximately 1·5-2 months under annual variations of daylength (Fig. 2). This fact was also demonstrated by Evans and Robinson (1980); the time lags in the pituitary response to GnRH of rams and ewes kept in an artificial light regimen of 6 months over a 2-year period were shorter for the former

than for the latter. From these data, it may be argued that gonadotrophic activity of male and female sheep do not have the same photoperiodic responsiveness to normal variations of daylength.

Distal Part: End of Gestation and Lactation

Préalpes du Sud ewes subjected to long days (15·5 L–8·5 D) from day 100 of gestation up to day 60 of lactation have significantly heavier twin lambs at lambing than similar ewes maintained under short days (8·5 L–15·5 D) although their food intake is identical (Bocquier 1985). Furthermore, this difference between twin birth weights of lambs born from long- and short-day ewes occurs regardless of the amount of body fat since this experiment was repeated at several seasons of the year (Fig. 3).
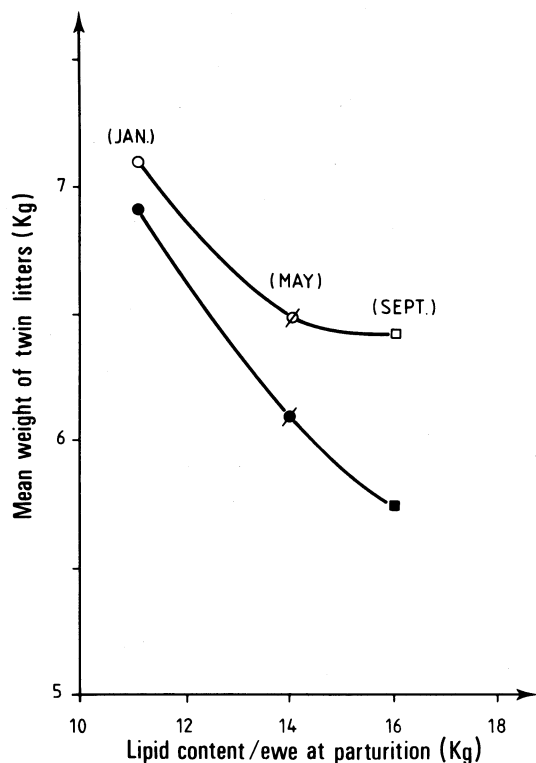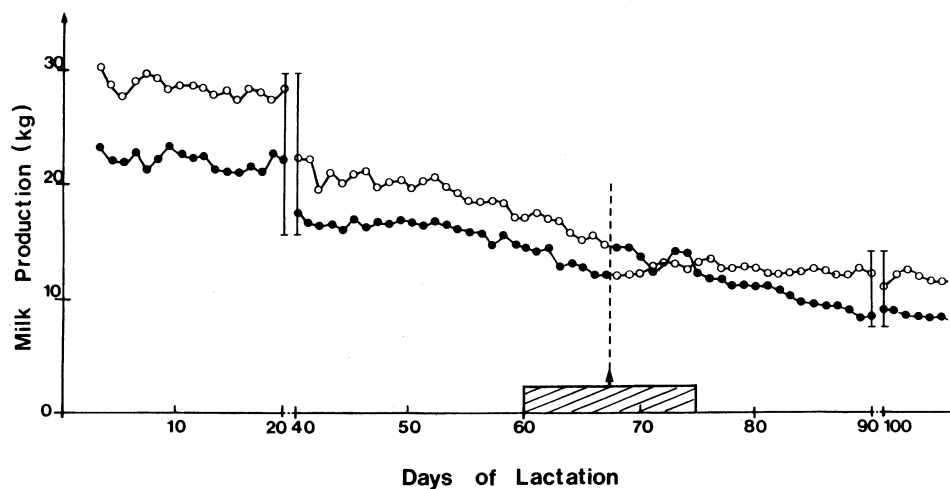

Fig. 3. Effect of photoperiod on lamb weight. At each season, whether in January, May or September, multiple birth weight is higher in ewes under long days (○ ∅ □) than in ewes under short days (● ◐ ■) (Adapted from Bocquier 1985.)

Also, ewes under long days systematically yielded more milk than those under short days right from the first day of lactation and milk yield curves were reversed very quickly after light treatments were reversed (Fig. 4). The difference in milk yield between the groups is 20% in favour of long-day ewes for the whole period. Even if the milk dry matter is decreased, the milk of long-day ewes had a higher energy content per day than did the milk of short-day ewes.
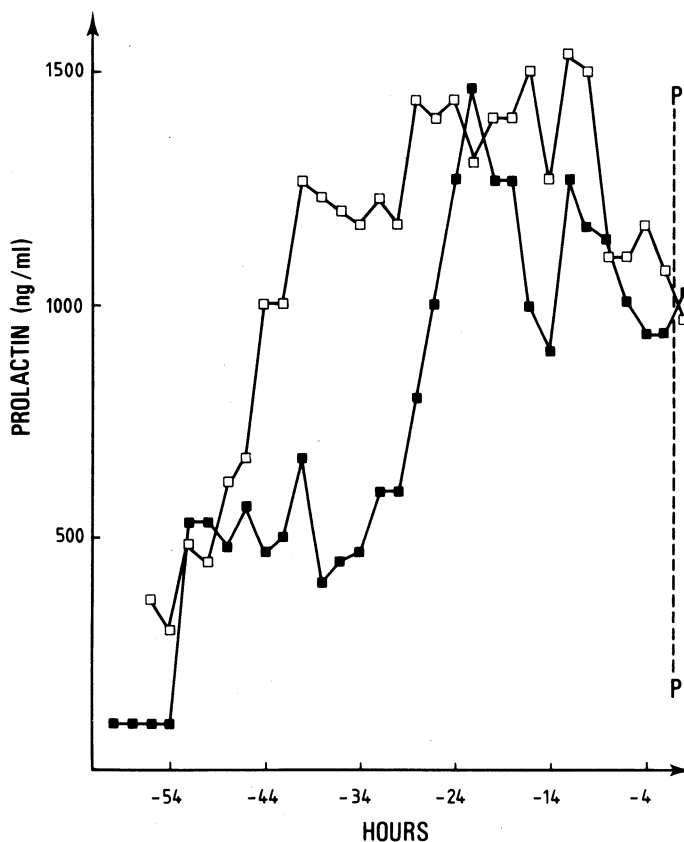
Ewes under long days have significantly higher OPL at day 130 of gestation and prolactin plasma levels than those under short days. Also, long days cause a 40% increase in the prepartum prolactin release and this increase begins earlier (Fig. 5). Thus, the wide differences between birth weight of twin lambs and milk yield at the onset of lactation result from variations in the hormonal status of the ewes induced by photoperiodic treatments during gestation and lactation. Finally prolactin plasma levels and milk production are significantly correlated during lactation.

Similar results concerning the effect of photoperiod on early lactation have been obtained in cattle (Peters *et al.* 1978, 1981), in goats (Terqui *et al.* 1984) and in sows (Mabry *et al.* 1982).

It can be concluded that photoperiod controls, at least partially, the distal part of the reproductive cycle in sheep.

Fig. 4. Effect of photoperiod on milk yield. Ewes kept under long days (O) yielded more milk than those under short days (●). When light treatment were reversed (cross-hatching), milk yield curves are also reversed very quickly. (Adapted from Bocquier 1985.)

Fig. 5. Effect of photoperiod on prolactin secretion at the end of gestation. Prolactin begins to rise at about 50 h before parturition (P). This increase is sudden and high in long-day ewes (□) and maximal secretion occurs about 44 h before parturition. In short-day ewes (■) prolactin reaches a maximum only 24 h before parturition. (Adapted from Bocquier 1985.)

Mechanisms of Photoperiodic Control of the Seasonality in Sheep Reproduction

Gonadotrophin secretion and release in sheep are mainly regulated by light and gonadal steroids.

Influence of Daylength Changes and Existence of a Light Mechanism Independent of Steroids

Stimulation of LH release is observed during decreasing daylength in intact rams submitted to light cycles with various periods from 2 to 8 months (Pelletier and Ortavant 1975a; Pelletier *et al.* 1985; Pelletier 1986). However, if the testis volume is taken as a criterion, the stimulation seems to occur during increasing daylength for short light cycles (4- and 3-month periods). This is due to the duration of spermatogenetic processes from spermatogonial divisions, stimulated by gonadotrophic hormones, to spermatids which constitute the major part of testicular parenchyma. Thus there is a phase lag if testis volume is taken as a criterion with short light cycles; but, on the whole, decreasing daylength appears to be constantly involved in the stimulation of LH release. However, a diminution of LH pulsatility is observed for short daylengths when the period of the light cycle is 6 or 8 months (Lindsay *et al.* 1984; Pelletier 1986).

A direct, i.e. steroid-independent, effect of light is shown by experiments done in both castrated rams (Pelletier and Ortavant 1975a) and spayed ewes (Evans and Robinson 1980; Robinson *et al.* 1985) submitted to 6-month light cycles. Under these conditions LH release is stimulated during decreasing daylength stages as in intact animals. However, increasing daylengths are not found inhibitory *per se* since an augmentation of LH release can be seen during this stage, but only when the period of the light rhythm is greater than 6 months. This was the case of rams kept under natural conditions (Pelletier *et al.* 1982) or under an 8-month light regimen (Fig. 6). All these results suggest that, in addition to the decreasing daylength effect, stimulation of the LH release could depend upon one or several other mechanisms.

A Light–Steroid Interaction of Gonadotrophin Release

The relative amplitude of changes in LH release during a photoperiodic cycle is found to be more marked in intact than in castrated rams (Pelletier and Ortavant 1975a) suggesting either the occurrence of a steroid effect or a light × steroid interaction. Robinson (1954) has shown first that it is possible to restore female receptivity in the castrated ewe by a sequence of progesterone and oestradiol treatment, and this inducibility of oestrous behaviour varies through the year (Reardon and Robinson 1961). Moreover, Robinson (1965), using tritiated oestradiol, showed that oestrogens accumulate in the pituitary and in some parts of the hypothalamus of the ewe. In this line of thought, it has been shown in the ram that the influence of testosterone on LH release varies according to daylength. The inhibition of LH release by testosterone is greater in rams under long days than in those under short days (Pelletier and Ortavant 1975b). Finally, these various results have brought strength to the following theory: (1) during decreasing daylength, LH release is stimulated and the negative feedback is reduced; (2) conversely, in increasing daylength, LH release is less and the feedback effect of steroids is increased (Pelletier and Ortavant 1975b) (Fig. 6). These results, confirmed later by Lincoln (1985) in the Soay ram, opened the way to the elegant experiments of Legan and Karsch (1980) in the ovariectomized ewe implanted with oestradiol. Under these conditions of constant oestradiol release through the year, plasma LH is decreased only at a time when the intact controls are in anoestrus and returns to a maximum during the sexual season. Similarly, in ovariectomized implanted oestradiol ewes submitted to alternations of long (16 h) and short (8 h) days every 3 months, plasma LH is lower during long days than during short days and the change in LH level occurs several weeks after the shift from long to short days (Legan and Karsch 1980).

The theory of light × steroid interaction explains satisfactorily when the gonadotrophin release is stimulated and when it is not. However, the shift from a stimulatory to a non-stimulatory situation is still unclear. So, in rams under natural conditions testis regression

occurs when daylength is still decreasing (Pelletier and Ortavant 1970), and there is a diminution of LH pulsatility for short daylengths in 6- or 8-month light cycles (Lindsay *et al.* 1984; Pelletier 1986).
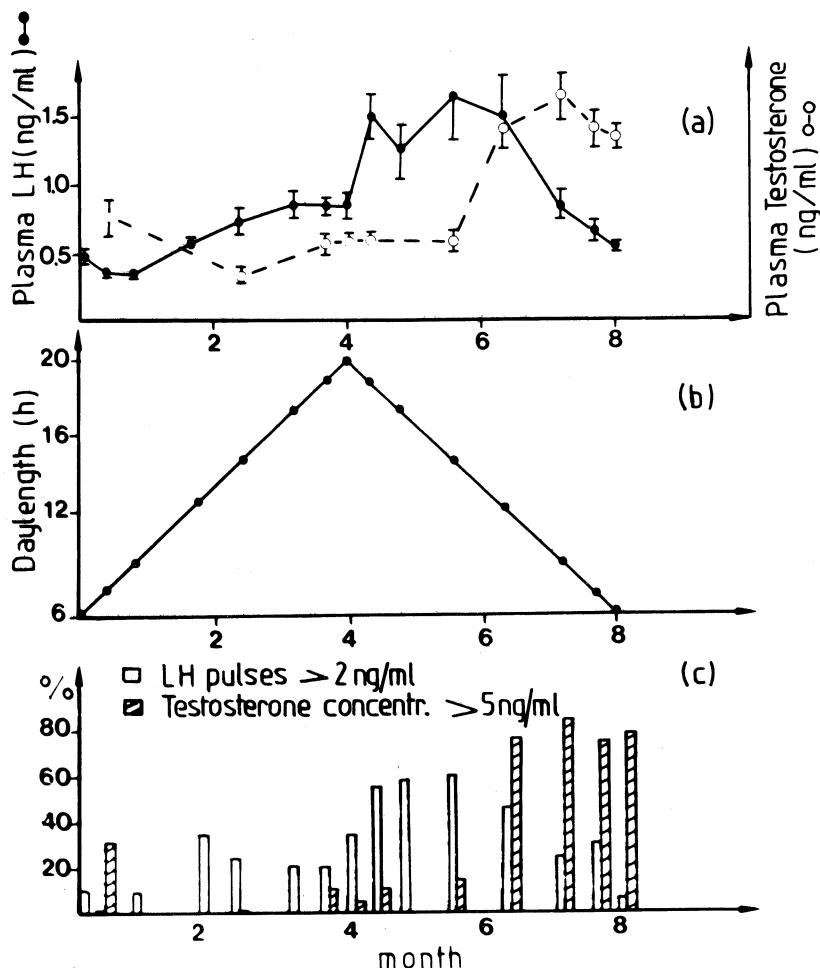

Fig. 6. Variations of LH and testosterone secretion under an 8-month light cycle. (*a*) Mean plasma LH (●) and testosterone (○) levels in Ile-de-France rams (*n* = 24). (*b*) Variations of daylength. (*c*) LH increases during decreasing daylength about 2 months before the testosterone augmentation. The damping of LH pulsatility coincided with the development of large testosterone pulses. (Adapted from Pelletier 1986.)

It can be speculated that the balance of the testosterone effect by decreasing photoperiods has a limit beyond which a feedback occurs. This is particularly clear in rams kept under an 8-month light regimen: after a period of several weeks during which LH and testosterone have a high pulsatility, amplitude of testosterone pulses increases abruptly and a prompt LH decline occurs (Pelletier 1986). Similarly opposite patterns of testosterone and LH in blood of Finish Landrace (Sanford *et al.* 1978) or Soay rams (Lincoln and Short 1980) have been also observed under natural conditions.

These results have given the basis for the attempts to abolish seasonality: the stimulation of gonadotrophins can be provided by decreasing daylengths, but this stage has to be brief in order to prevent the onset of a negative feedback effect.

A Step Forward to the Abolition of Sheep Seasonality

Frequent and brief stimulations of LH release can be provided using regimens of increasing

and decreasing daylengths whose periods are reduced from 6 to 4, 3 or even 2 months. The testis weight of rams follows the photoperiodic changes in the first three cases but it increases and stays close to the maximum in the last one (Pelletier *et al.* 1985). At the present time rams have been showing a persistent high testis weight for more than 2·5 years.

Similar results have been obtained in ewes by Rougeot (unpublished data), using the same photoperiodic protocols: with a 2-month cycle, oestrus occurs during lengthening days as well as during shortening ones. Moreover, 80% of theoretically possible oestrous periods were detected during the period of the experiment, suggesting that photorefractoriness may be overcome.

The use of alternations of 1 month of constant long days with 1 month of constant short days also gives similar results in rams. Under short light cycles, the magnitude of changes in plasma LH and testosterone is low, while the frequency of low amplitude pulses is high (Pelletier and Almeida 1987 and unpublished data). Semen characteristics (high number of spermatozoa per ejaculate and low number of abnormal spermatozoa) are similar in rams under short light cycles and those collected during the sexual season. The abolition of sheep seasonality in rams kept under artificial light regimens is a step forward to persistent breeding under farm conditions.

Photoperiodic Time Measurement in Sheep
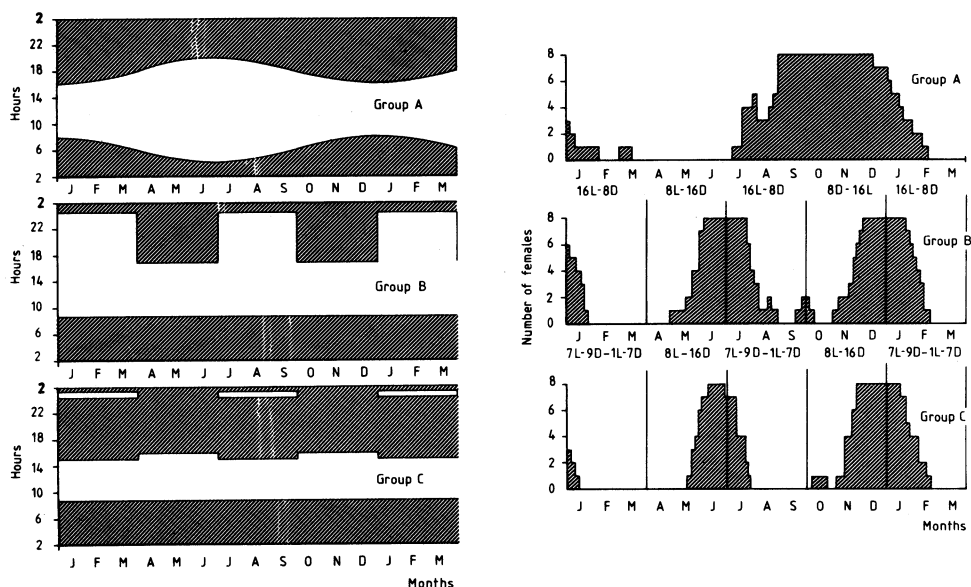### Existence of Circadian Rhythm of Photosensitivity

The preceding results raise the question of how sheep measure photoperiodic time. An early hypothesis assumed that the total duration of the light or dark period was measured by some sort of hourglass timing mechanism. But now Bunning's hypothesis is usually evoked to explain photoperiodic time measurement in mammals. According to this hypothesis, an endogenous circadian rhythm of photosensitivity is involved. In an internal coincidence model light serves a dual role. First, it entrains this circadian rhythm of photosensitivity to itself, and second, when external light is coincident, or not coincident, with a photoinducible phase of that rhythm, the physiological response is stimulated or not stimulated. Thus, the critical factor is the phase relationship between light and the circadian oscillator involved in the transmission of information about daylength to the hypothalamic–pituitary–gonadal axis.

This hypothesis is now supported in sheep by results obtained by using experimental light–dark cycles referred to as resonance or night-interruption experiments. In resonance experiments, sheep are exposed to a series of light–dark cycles where a fixed short photoperiod is coupled to varying durations of darkness such that the period of the light–dark cycle is lengthened by increments of 12 h. The results of resonance experiments indicate that neither the duration of light nor the duration of darkness, nor a ratio between the two is the determining factor for inducing photoperiodic responses in testis weight, sexual skin flush, secretion of prolactin and melatonin in the ram (Almeida and Lincoln 1982) or oestrus and secretion of prolactin and melatonin in the ewe (Ravault and Thimonier, unpublished data). But the results indicate that time-keeping involves a response that varies on a circadian basis.

In night-interruption experiments, animals are exposed to short days with the night being interrupted by a short pulse of light, for example 1 h of light given 16 h after the beginning of a short day of 7 h. Such a light treatment leads to a long-day response of ovarian activity in ewes (Fig. 7). In rams, Pelletier and Thimonier (1987) used a pulse of light mobile in relation with a short day of 7 h, both fractions mimicking normal variations of daylength in a 6-month cycle (Fig. 8). Rams which received light in two fractions presented testis weight variations which were similar to those of controls submitted to changes of light given in one block.

From all these experiments it can be concluded that daylength is not measured by the total duration of exposure to light but by the illumination of two special set points during the day. One of them probably entrains a circadian rhythm of photosensitivity and the other may be important for physiological responses by its position in relation to this circadian rhythm and the photoinducible phase. Such a photoinducible phase has been detected for prolactin

secretion in the ram (Ravault and Ortavant 1977; Ravault *et al.* 1981), and in the ewe (Thimonier *et al.* 1978), and for LH secretion in the ram (Pelletier *et al.* 1981).
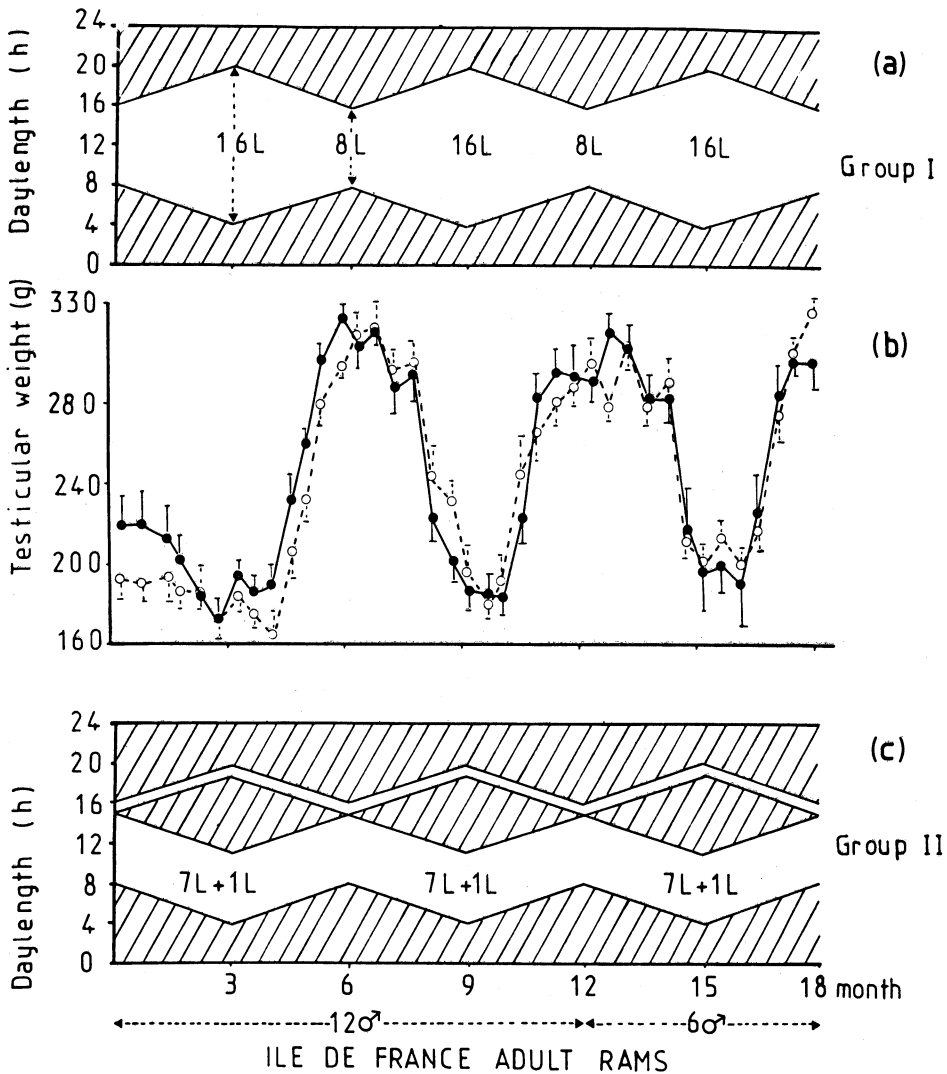

Fig. 7. Ovarian activity of ewes submitted to a 'night-interruption' experiment (cross-hatching, darkness; no hatching, light.) Left panel: Experimental protocol: group A (8 ewes) submitted to normal variations of daylength; group B (8 ewes) submitted to alternations of 3-month periods of short days (8 L –16 D) and long days (16 L –8 D); group C (8 ewes) submitted to alternations of 3-month periods of short days (8 L –16 D) and of a light treatment mimicking long days (7 L –9 D–1 L –7 D). Right panel: Number of ewes with ovarian activity in each group along the experiment. The ewes in group C measure the light treatment (7 L –9 D–1 L –7 D) as a long day.

Transfer of Photoperiodic Information

There is now good evidence implicating the pineal gland in the transfer of photoperiodic information to the hypothalamo–pituitary axis (see reviews: Karsch *et al.* 1984; Arendt 1986).

Among the main indoleamines secreted by the pineal gland, melatonin has been the most studied in sheep. Many results provided evidence that melatonin is secreted during the dark period of the day; its level is very low during the light period (Rollag and Niswender 1976). So, the duration of the nocturnal melatonin rise may constitute the message whereby the pineal mediates photic regulation of hormonal secretion. Nightly infusion of melatonin in a short-day pattern (16-h duration) into pinealectomized ewes resulted in high frequency LH pulses. Conversely, no LH pulses were observed in any of the pinealectomized ewes receiving melatonin over a long-day pattern (8-h duration) (Karsch *et al.* 1984; Bittman *et al.* 1985).

We have seen that daylength is measured between two illuminated set points during the day even if there was no light in the interval between them. In the same way, it seems that melatonin plasma levels do not have to be permanently low during the 'subjective' light day. Using night-interruption experiments in ewes, Brinklow *et al.* (1984), Earl *et al.* (1985), and Ravault and Thimonier (unpublished data) have shown that plasma melatonin is low in all ewes during the two light fractions. But during the second night fraction, plasma melatonin levels remain low (Brinklow *et al.* 1984; Earl *et al.* 1985) and/or low or highly variable between ewes (Ravault and Thimonier, unpublished data). This could be related to the position of the light pulse. Nevertheless, in the experiments of Ravault and Thimonier, all these ewes

Fig. 8. Testicular weight variations (*b*) in control group I (●) and experimental group II (○) rams according to photoperiodic daylength changes (*a* and *c*). (From Pelletier and Thimonier 1987, with permission.) Cross-hatching, darkness; no hatching, light.

(with low or variable plasma melatonin levels during the second night fraction) reacted in the same way with regard to the ovarian cycle and prolactin secretion. It was as if melatonin secretion during the second dark fraction mattered little (Fig. 9). What seemed important was the disappearance of that secretion during two set points during the day.

But whatever the mode of action of melatonin, its administration, either by infusion, ingestion, injection or even constant-release devices allows short days to be mimicked (see review of Arendt 1986). The alternation of periods of utilization of melatonin for mimicking short days and of utilization of light pulse for mimicking long days may allow a control of the reproductive cycle in sheep and goats without having to use buildings that are light-proof (Chemineau *et al.* 1986).
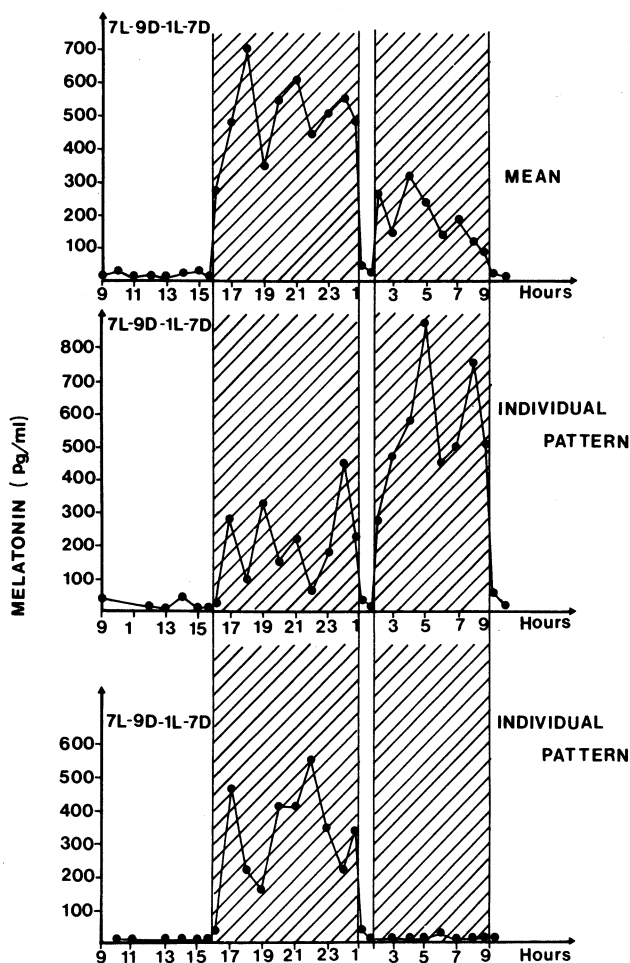
Fig. 9. Mean and two individual plasma melatonin patterns in ewes submitted to a daily night interruption treatment (7 L –9 D–1 L –7 D). Ewes fall into two groups with regard to plasma melatonin levels during the second dark fraction: one with a high level and one with a low level, as during the light fraction. But all these ewes reacted as animals under long days as to the ovarian activity. (Unpublished data of Ravault and Thimonier and published here with permission.)

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