

## Short light cycles induce persistent reproductive activity in Ile-de-France rams

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**Summary.** European breeds of rams appear to be responsive to photoperiodic changes even though there are large differences between breeds in the timing and amplitude of endocrine (LH and testosterone) and gametogenetic variations before the sexual season. Light regimens such as 6-month light cycles or alternations of constant short and long days every 12–16 weeks are able to entrain the parameters of sexual activity. In these regimens in which the period of the light cycle is shortened, LH release is markedly stimulated during decreasing daylength and evidence is presented, from the relationship of LH and testosterone patterns, that the dampening of LH stimulation could simply result from the effect of steroid feedback. However, there is a gap of several weeks between the maximum LH and testosterone concentrations during which testis growth occurs. Experiments were conducted with Ile-de-France rams, markedly seasonal breeders, in which the period of the light cycle was decreased, in different groups of animals, from 6 to 4, 3, 2 or 1 month. Rams submitted to the three light regimens with the longest periods presented testicular variations which paralleled those of the photoperiod, but those kept in the two regimens with the shortest periods had a progressive increase in testicular weight up to the maximum value (300–350 g) with no further major changes. Therefore, in rams kept in 2-month light cycles, testicular weight remained constant for twelve successive cycles (2 years). LH and testosterone plasma measurements indicated that LH was sufficiently stimulated to maintain testicular development during each decreasing daylength phase but that the stimulation was shifted before testosterone could reach levels at which feedback effects could be exerted. However, all the measures of sperm production were at values characteristic of the sexual season. Similar testicular weight maintenance was also obtained in rams submitted to a regimen in which short days (8L:16D) alternated every month with a split photoperiod interpreted as a long day (7L:8D:1L:8D). It is concluded that short light cycles are able to induce persistent reproductive activity in Ile-de-France rams, which may have practical applications in sheep production systems.

### Introduction

Rams exhibit seasonal variations in both behaviour and testicular endocrine and gametogenic activity. Generally both parameters are high at the end of summer and in autumn and low at the end of winter and in spring, thus suggesting a role of photoperiod. In the ram, it has been proposed that light acts on gonadotrophin release, which in turn controls reproduction according to (i) a gonad-independent mechanism and (ii) a change in the magnitude of feedback in relation to the increase or decrease of daylength (Pelletier & Ortavant, 1975a, b). However, in view of the existence of different mechanisms, it is important to distinguish induction of seasonal activity from suppression. The first aim of this paper is therefore to review our knowledge on both the inductive and inhibitory effects of light on LH release and testicular activity. Seasonality is also however a brake

to breeding throughout the year, and the second aim is to present a summary of the attempts made to abolish periodic inactivity.

In the first place it is of interest and importance to comment on the natural seasonal variations of LH and testosterone, and of testicular weight. The latter provides, mainly through changes in spermatogenic activity, a reflection of gonadotrophin release.

### Seasonality of LH release and testicular activity in rams of different breeds

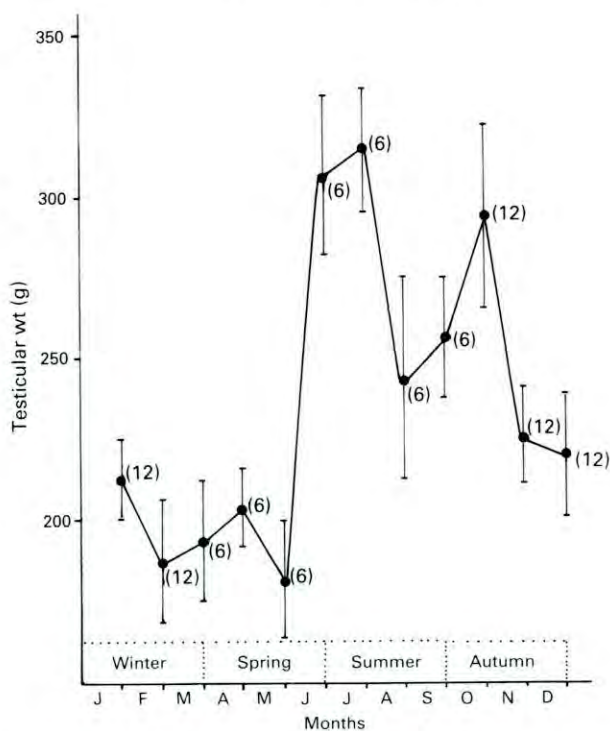
#### *Seasonality of LH release*

In the great majority of rams plasma LH is low during the winter and early spring and high during the summer months, before the breeding season. However, the results are far from homogeneous, perhaps due to different breeds, latitude or protocol (number of animals involved and frequency of bleeding). In Ile-de-France and Préalpes-du-Sud rams, the frequency of LH pulses increases in spring and, at least in the latter breed, remains high until the beginning of autumn (Pelletier *et al.*, 1982). An increase in the number of LH pulses or of the mean LH concentration is also observed before the summer solstice in Soay rams (Lincoln, 1976) and in Polled Dorset and Romney rams (Barrell & Lapwood, 1978/1979). However, in Finnish Landrace males no increase of LH pulsatility is observed until September (Sanford *et al.*, 1977) and the height of LH pulses increases significantly in July and declines quickly during autumn (Sanford *et al.*, 1984). From these data it is hard to compare with precision the photoperiodic effects on LH release in different breeds. This leads us to consider the seasonal changes of testicular values, even though they can be thought of as more distal markers of the light influence than LH pulsatility. Amongst these measures testosterone concentrations and testicular weight are the best documented.

#### *Seasonality of testicular activity*

*Testosterone release.* A testosterone pulse follows each LH pulse but the amplitude of the testicular response to LH varies greatly through the year and maximal plasma testosterone concentrations are not coincident with maximal plasma LH but occur later. In Ile-de-France and Préalpes-du-Sud rams, mean testosterone concentrations begin to increase around the middle of spring (Pelletier *et al.*, 1982). Similarly, in almost all breeds of sheep plasma testosterone starts to increase before the summer solstice (Suffolk: Schanbacher & Lunstra, 1976; Merino, Polled Dorset and Romney: Barrell & Lapwood, 1978/1979; D'Occhio & Brooks, 1983; Soay: Lincoln, 1976). Following the late LH increase, plasma testosterone augmentation is delayed until September in Finnish Landrace sheep (Sanford *et al.*, 1977), although in another study the initial increase in this breed is found somewhat earlier (Schanbacher & Lunstra, 1976). In all these cases, maximum plasma concentrations are found at the end of summer and autumn. A clearly different phenomenon is seen in Ouled-Djellal rams from Algeria in which testosterone concentrations increase as early as mid-winter, and are maximum in early summer and minimum in mid-autumn (Darbeïda & Brudieux, 1980).

*Testicular weight.* The testis has the advantage of integrating different facets of LH release and of being the target of both LH and FSH. It could therefore be considered as a representative parameter of male seasonal activity. Generally, testicular weight is highest at the end of summer and the beginning of autumn and lowest at the end of winter. Testis redevelopment begins in early summer in Merino and Finnish Landrace breeds (Islam & Land, 1977). Significant testis growth occurs from the beginning of June onwards in Ile-de-France (Fig. 1) (Pelletier & Ortavant, 1970) and Suffolk or Suffolk crosses (Dufour *et al.*, 1984). Finally, in rams of some breeds such as the Soay (Lincoln & Short, 1980) or Préalpes-du-Sud (Pelletier *et al.*, 1981), testicular growth begins still earlier, clearly before the summer solstice and well before the time of reproduction.



**Fig. 1.** Seasonal variations of testicular weight in Ile-de-France rams; testicular weights are adjusted by covariance to body weight. Values are the mean  $\pm$  s.e.m. for the no. of animals in parentheses. (After Pelletier & Ortavant, 1970.)

From the preceding data it is clear that all breeds of rams exhibit seasonal variations of both endocrine and sexual activities. However, many studies underline breed differences with respect to either the time of the seasonal gonadotrophin increase or testicular growth or the duration of sexual activity (Islam & Land, 1977; Barrell & Lapwood, 1978/1979; Dufour *et al.*, 1984). The magnitude of these differences can be marked if one considers the increase of LH pulsatility in early spring for Préalpes-du-Sud (Pelletier *et al.*, 1982) *versus* summer for Finnish Landrace rams (Schanbacher & Lunstra, 1976; Sanford *et al.*, 1977). If light is generally considered as the major cue driving reproduction through the stimulation of the hypothalamo-hypophysial system in European breeds, important differences in the response of the system can be anticipated. Furthermore, some breeds such as the Merino with a weak seasonality, should have a decreased sensitivity to light since seasonal variations were relatively similar when studied at 55°N (Islam & Land, 1977) or 35°S (D'Occhio & Brooks, 1983), i.e. under a very different amplitude of photoperiod change. All these phenomena suggest that sheep of particular breeds retain some intrinsic property of sensitivity to light.

The influence of light is still less evident at lower latitudes. For example, in Ouled-Djellal rams, the shift in seasonal endocrine profiles is sufficiently marked compared to European breeds as to suggest a role of temperature as a predominant cue (Darbeida & Brudieux, 1980). In the Barbarine or Noire de Thibar rams (35°N, Tunisia), seasonal variations are extremely slight and at the limit of significance (Mehouachi, 1985). However, precise information concerning breeds from tropical or equatorial countries is still required.

In conclusion, in spite of the above mentioned differences, seasonality is thought to be a general phenomenon in European breeds of sheep and all of them appear to be responsive to photoperiod change. This is particularly clear when animals are under artificial light regimens as indicated below. However, in breeds originating from lower latitudes, where photoperiodic changes are moderate, seasonality is much weaker. One can therefore conclude that seasonality is perhaps not a specific trait of sheep but is likely to be related to adaptation to a particular photoperiodic environment.

#### *Light entrainment of LH release and testicular activity*

Attempts to drive the activity of the hypothalamo-hypophysial axis, and thus gonadal activity, by artificial light regimens, have been conducted using three basic types of protocol. The first one involves a simple 6-month shift in the annual daylength change in order to induce full activity in males at the time when they are normally quiescent. The second one involves a shortening of the period of the light cycle to multiply the number of sexual seasons during the year. The last procedure includes a decrease of the duration of the light cycle with a simplified photoperiodic schedule limited to abrupt switches from long to short days and *vice versa*.

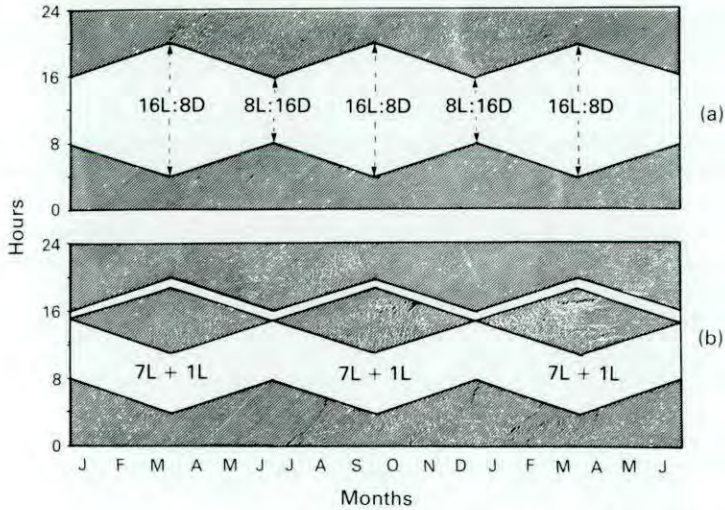
*The annual cycle with a 6-month shift.* In Ile-de-France rams, a 6-month shift of the normal annual change in daylength produces an equivalent shift in the pattern of LH release together with testicular development and maximal production of testosterone (Alberio, 1976). Under a similar light schedule, another study also showed that weekly sperm production is maximal in the photoperiodic autumn, whatever the actual time of year at which decreasing daylength occurs (Colas *et al.*, 1985). This protocol is used with success in different artificial insemination centres for sperm production in France (G. Colas, personal communication). However, to study photoperiodic mechanisms, workers have frequently used light regimens with a shortened period.

*Influence of sinusoidal light cycles with shortened periods.* A light regimen which mimics the normal annual photoperiodic changes in 6 months leads in Ile-de-France rams to two 6-month cycles of testicular weight in 1 year (Ortavant & Thibault, 1956). The testes begin to grow 1.5 months after the shift from long to short days, i.e. when daylength is 12 h. The maximum number of primary spermatocytes at the leptotene stage is observed when decreasing daylength is 10 h (Ortavant, 1961) and finally testis weight is greatest in short days (8 h). Similar effects of 6-month light cycles on sperm production have also been shown in Suffolk rams (Jackson & Williams, 1973).

Measurements of mean plasma LH in intact and castrated Ile-de-France rams indicate that the levels are highest during decreasing daylength (Pelletier & Ortavant, 1975a) as a result of an increase in pulsatility (Lindsay *et al.*, 1984). An increase in testosterone release also occurs in decreasing daylength in Finnish Landrace rams exposed to the same light regimen (Sanford *et al.*, 1978). However, the number of LH pulses is lowest during increasing daylength.

*Alternation of constant long and short days.* When Soay rams are exposed to a light regimen whereby constant long days (16 h) switch abruptly to short days (8 h), the switch is followed in 6–12 days by an increase in mean plasma LH concentration and LH pulsatility, followed about 3 weeks later by an enlargement of the testes (Lincoln, 1976; Lincoln & Peet, 1977). Alternating short and long days every 16 weeks leads to an entrainment of LH, testosterone and testicular weight. Similar results were observed by D'Occhio *et al.* (1984) for rams of different breeds such as Polled Dorset, Finnish Landrace, Rambouillet and Suffolk when exposed to alternating short and long days every 12 weeks.

In summary, all the results to date obtained from the use of artificial light regimens with shortened periods indicate that photoperiodic cycles are able to entrain the activity of the hypothalamo-hypophysial axis. In all cases stimulation was observed during decreasing daylength. In addition, this indicates that animals are able to measure daylength and to adjust their endocrine activity accordingly. The mechanism of daylength measurement therefore appears to be of crucial importance.



**Fig. 2.** A 6-month light cycle in which (a) daylength varies from 8 to 16 h and *vice versa* or (b) the light photoperiod is provided in two blocks, one of 7 h adjusted to the dawn of the previous group and the other one of 1 h adjusted to dusk.

#### Daylength measurement in Ile-de-France rams

Ravault & Ortavant (1977) have shown that 8 h light given in two blocks (7L:9D:1L:7D) are able to mimic a long day and to stimulate prolactin release in Préalpes-du-Sud rams. We have also examined the effect of a split photoperiod on the testicular weight of Ile-de-France rams by using an original protocol in which the second block (or 'light pulse') was mobile.

One group of 12 rams was exposed to a 6-month light cycle in which daylength varied from 8 to 16 h in 3 months and from 16 to 8 h in the other 3 months (Fig. 2a). Another group (N = 12) received light in two blocks, one of 7 h adjusted to 'dawn' of the previous group and a pulse of 1 h adjusted to 'dusk' as indicated in Fig. 2(b). Testicular weight changes were strictly identical in the two groups and similar to the pattern shown in Fig. 4(a). Minimal values, 170–200 g, were observed just after the longest days and maximum values, 300–320 g, were obtained after the shortest days. Furthermore, in the group of rams receiving the light in two blocks, testicular patterns were similar in all individuals. These results confirm previous ones and show that: (1) daylength is measured between two limits even if the interval between them is not always illuminated, (2) the measurement of daylength is homogeneous between animals since apparently none of them took the pulse for the main dawn (Thimonier *et al.*, 1985; J. Pelletier & J. Thimonier, unpublished results). The importance of dawn as a reference mark for LH release is substantiated by the patterns of LH pulse frequency through the day: both in winter and in summer the maximum number of pulses is found 3–4 h after dawn (Ortavant *et al.*, 1982). Furthermore, experiments with split photoperiods show that a 1 h light pulse given each day 16–17 h after dawn stimulates LH release and testicular weight development. Light pulses given at other times of the night are less efficient, or unable to stimulate LH and from these results the existence of a circadian rhythm of sensitivity was postulated (Pelletier *et al.*, 1981). However, the stimulation observed when the photosensitive phase is illuminated tends to vanish in a few weeks. This could be due to a displacement of the photosensitive phase relative to dawn or to the development of a so-called refractoriness.

### Is photorefractoriness a phenomenon related to steroid feedback in the ram?

#### *Light regimens and appearance of photorefractoriness*

Finnish Landrace and Soay rams kept for several years under a constant light schedule exhibit testicular changes with a period of 35–40 weeks (Howles *et al.*, 1982; Almeida & Lincoln, 1984) as if animals of these normally light entrained breeds have an endogenous rhythm of activity. It therefore appears unrewarding to try to identify a definitive stimulatory photoperiod. Although the mechanism(s) by which the endogenous rhythm is expressed is still unknown, it nevertheless recalls a general phenomenon detectable in almost all light regimens studied.

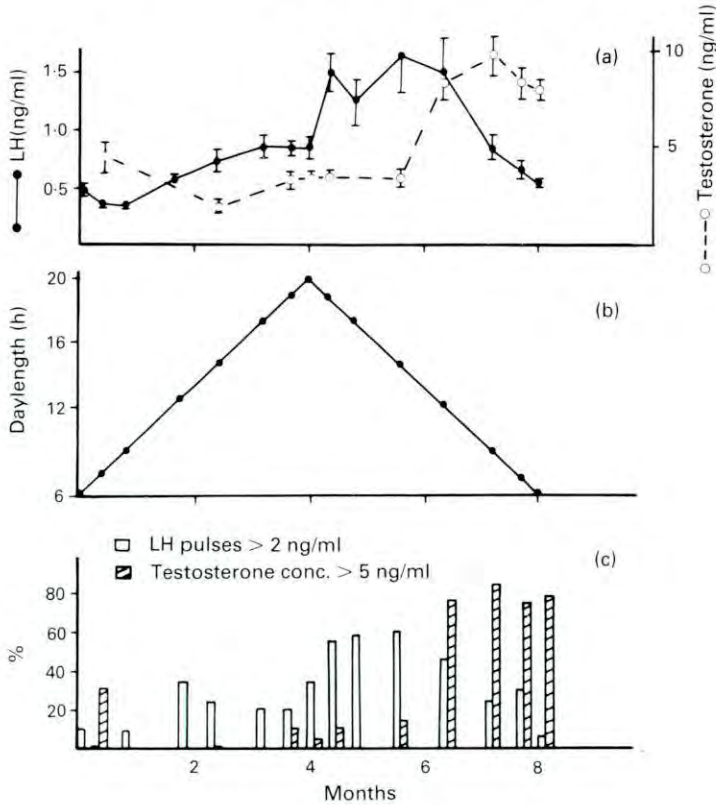
When Soay rams are transferred in early winter from a natural to an artificial constant 8L:16D regimen, photorefractoriness to initially stimulatory short days is shown by a delayed testicular development (Lincoln, 1980). Similarly, when rams are switched from long to short days, LH release and testicular development occur but both measures begin to decline before the next switch from short to long days (Lincoln & Short, 1980; D'Occhio *et al.*, 1984). A diminution of LH pulsatility is also observed in Ile-de-France rams kept under a 6-month light regimen, when daylength decreases from 10 h 40 min to 8 h (Lindsay *et al.*, 1984). Finally, when rams are kept under natural daylength, regression of testicular weight clearly begins before the winter solstice (see Fig. 1). Thus, whilst LH release and testicular weight are initially stimulated by decreasing daylength, photorefractoriness occurs for both.

Conversely, photorefractoriness also occurs with constant long days or increasing daylength in a sinusoidal 6-month light regimen and leads to an increase in LH pulsatility. It is therefore possible that the increase in LH pulse frequency and the early testicular redevelopment observed in late spring in rams under natural conditions are also due to winter photorefractoriness. This phenomenon is examined below in an experiment using an 8-month light cycle.

*Photorefractoriness to constant incremental increases and decreases in daylength and relationship to steroid feedback.* In this experiment, the daily light increment and decrement was twice the normal equinoctial values in order to magnify the putative intrinsic properties of increasing and decreasing daylengths. In addition, an 8-month period of the light cycle was chosen so that photorefractoriness could be detected easily. With these parameters the range of daylength variations is 6–20 h (Fig. 3a).

Results indicated that mean LH release and the number of LH pulses increased significantly when daylength was greater than 12 h (Fig. 3b). However, the amplitude of the pulses was low. Although a testosterone pulse normally follows each LH pulse, the increase in mean testosterone level was negligible. As soon as daylength declined from 20 h to 18 h 30 min, there was an abrupt increase in the magnitude of LH pulses (Fig. 3c), resulting in a steep augmentation of the mean plasma concentration. Then, when decreasing daylength reached 12 h, testosterone pulses and the mean plasma value increased in their turn and, at that time, a concomitant decline in LH release occurred.

These results indicate that (a) LH release rises slowly with increasing daylength either by the absence of a strong testosterone feedback since the levels are low at that time, and/or by illumination of the photosensitive phase; conversely, LH release rises quickly in decreasing long daylength, suggesting the existence of at least two mechanisms; (b) the abrupt decline in LH release could essentially be due to high testosterone levels; and (c) there is a gap of about 2 months between the maximum LH and testosterone concentrations in plasma (Pelletier, 1986). This last finding suggests that under light cycles in which the period is greater than 4 months, photorefractoriness is likely to occur. Photorefractoriness to increasing daylength could be equivalent, at least in part, to a reduced steroid feedback, whereas it was the result of strong steroid feedback in decreasing daylength. The opposite patterns of LH and testosterone release are observed in Finnish Landrace (Sanford *et al.*, 1978) and Soay rams (Lincoln & Short, 1980). These conclusions on the whole are in agreement with classical endocrine data and do not preclude the intervention of other



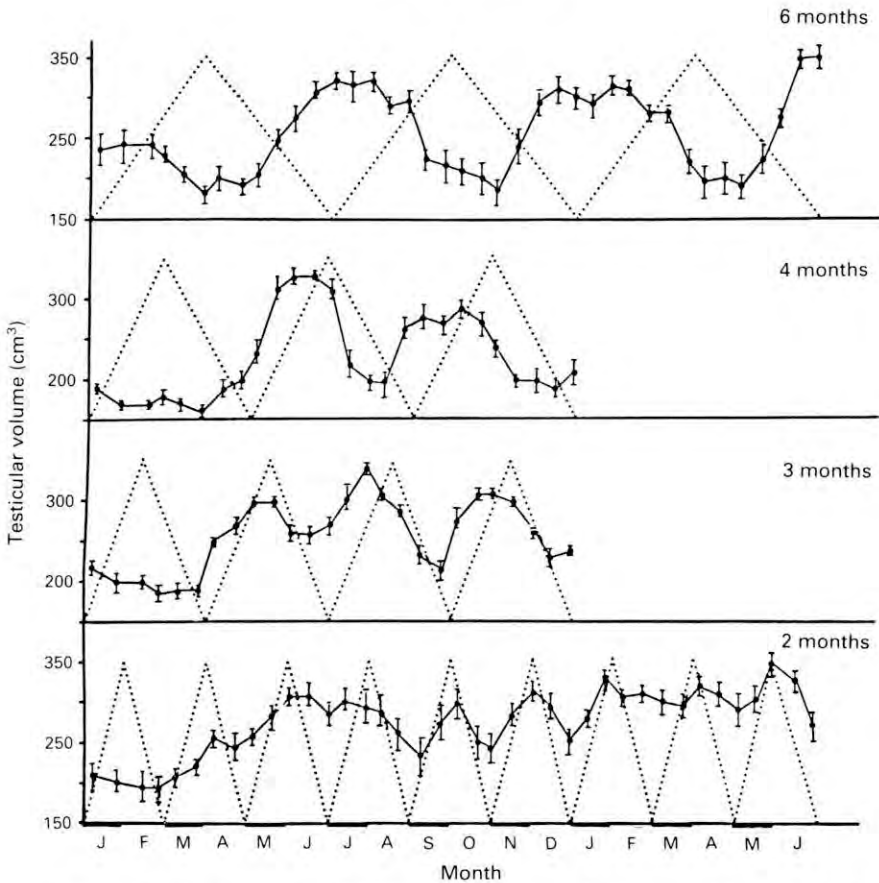
**Fig. 3.** Changes of plasma LH and testosterone concentrations (a) and LH pulses > 2 ng/ml and testosterone pulses > 5 ng/ml (c) in 12 Ile-de-France rams according to (b) daylength variations in an 8-month light regimen. In (a) values are mean  $\pm$  s.e.m. (After Pelletier, 1986.)

mechanisms of LH stimulation when schedules imply constant or sinusoidal light regimens of long duration.

#### Abolition of seasonal variations in testicular function in Ile-de-France rams

Since the previous results indicated that photorefractoriness requires at least 2 months to develop, it is pertinent to check the effects of shorter and shorter light cycles. Furthermore when the period of the light regimens decreases from 12 to 8 or 6 months the stimulation of LH release tends to be confined to decreasing daylengths whilst increasing daylengths appear not to be stimulatory and could allow 'relaxation' of hypothalamo-hypophysial activity.

*Influence of shortened light cycles on testicular weight, LH and testosterone release.* The following protocol was used in four groups of 6 Ile-de-France rams submitted to an artificial light regimen. Daylength varied from 8 to 16 h and *vice versa*. The period of the light cycle was 6, 4, 3 or 2 months and testicular weight was measured every 2 weeks for 18, 12, 12 and 18 months respectively. Changes in testicular weight were analysed using an harmonic regression analysis following the model  $y(t) = \mu + \alpha \sin(2(\pi t/\tau) + \phi)$  where  $\mu$ ,  $\alpha$ ,  $\tau$  and  $\phi$  are the mean, amplitude, period and phase respectively (Marquardt, 1963).



**Fig. 4.** Variations of testicular weight (—) according to the light regimen (···) in which the period of the cycle is 6, 4, 3, or 2 months. There are 6 rams in each group and values are the mean  $\pm$  s.e.m. (From Pelletier *et al.*, 1985, with permission.)

The results (Fig. 4) clearly indicate that rams kept in the 6-, 4- and 3-month light regimens exhibited seasonal variations in testicular weight. Conversely, rams kept in the 2-month light regimen showed a progressive increase in testicular weight which finally remained steady close to the maximum level. When the period of the light cycle decreases the adjusted mean testis weight increases while the magnitude of variations declines (Pelletier *et al.*, 1985). Results obtained with another group of rams kept for 1 year under a regimen in which the period was 1 month were similar to those obtained in rams under 2-month cycles. In the 6-month group, the changes in testicular weight fit the sinusoidal model ( $R^2 = 0.89$ ) and the magnitude of variations, i.e. twice the computed amplitude, was about 130 g (Table 1). Furthermore, the phase shift between the maximum of daylength and that of testis weight was 105 days. On the other hand, the values obtained in rams kept in the 2-month and 1-month light cycles do not fit the model ( $R^2 < 0.20$ ) and a phase shift with the light regimen cannot be computed. However, it is clear that the amplitude of testicular change was 4 times less than in the group of rams exposed to the 6-month cycle.

Plasma LH and testosterone concentrations were studied on four occasions (daylength: 8 h, 12 h increasing, 16 h and 12 h decreasing) during two successive cycles in the rams kept in the 2-month light cycles. The pooled data for equivalent daylengths are given in Table 2 and show that



**Table 1.** Variation in testis weight of Ile-de-France rams according to different light regimens: determination of the coefficient between the observed and computed curves, mean, amplitude, period and phase of the computed curves as a function of the period (T) of the light cycle

Period of the light cycle (months)	R <sup>2</sup>	Mean (g)	Amplitude* (g)	Period (days)	Phase (days)
6	0.89	262 (256-268)	66 (57-74)	186 (181-191)	-105 (-113 to -97)
2	0.19	297 (289-304)	18 (6-30)	60 (58-61)	(-)
1†	0.15	255 (240-270)	15 (6-36)	54 (42-64)	(-)

Values in parentheses are confidence limits ( $P = 0.05$ ).

\*Half of the difference between minimal and maximal testicular weight.

†Animals in this group were 2 years younger than in the two other groups.

**Table 2.** LH pulsatility, mean plasma LH and testosterone concentrations according to daylength in Ile-de-France rams (6/group) exposed to 2-month light cycles\*

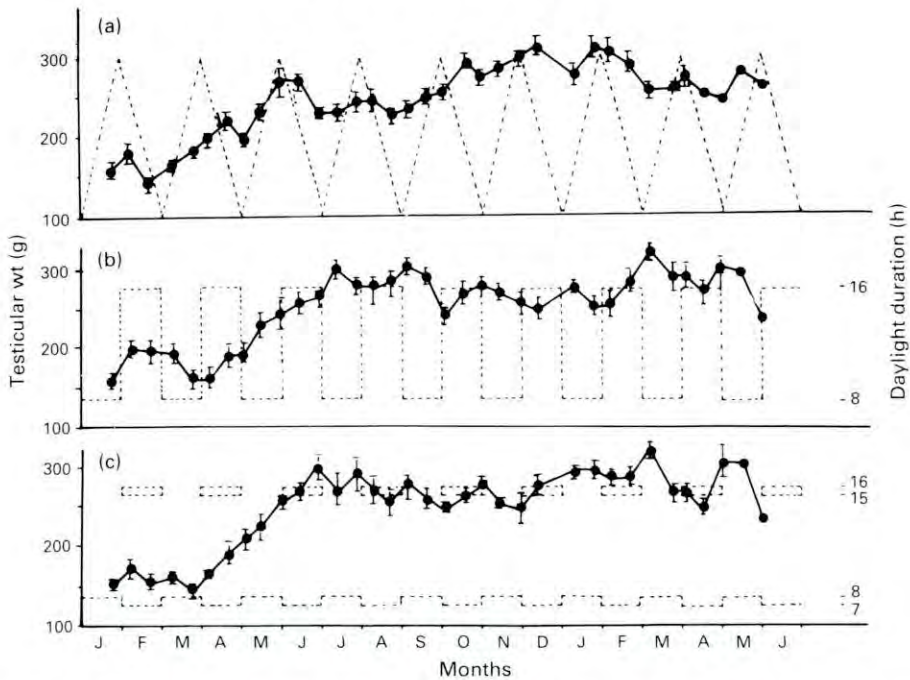
Daylength (h)	No. of pulses/8 h	Plasma LH (ng/ml)	Plasma testosterone (ng/ml)
8	2.5	1.43 ± 0.05†	1.75 ± 0.07
12 (increasing)	2.4	1.19 ± 0.03	1.85 ± 0.08
16	2.4	1.08 ± 0.03	1.73 ± 0.09
12 (decreasing)	1.8	1.00 ± 0.02	1.24 ± 0.06

\*Mean or mean ± s.e.m. of the pooled data collected during two successive light cycles.

†Variations according to daylength significant ( $P < 0.05$ ).

the number of LH pulses on the one hand, and mean plasma concentrations of LH and testosterone on the other hand, were highest when rams were kept in short daylengths (8 h) resulting from the previous stimulation by decreasing daylength. However, only the mean values differed significantly and the extent of changes, 43 and 29% for LH and testosterone respectively, are far less than those recorded either under natural daylength (Schanbacher *et al.*, 1987) or in an artificial light regimen in which the period is at least 6 months (see Fig. 4). Similarly, the ratio of the highest to the lowest LH pulse frequency during the photoperiodic cycle is only 1.37 as compared to 1.66 when Ile-de-France rams are kept in natural daylength (Pelletier *et al.*, 1982) and 8.00 when they are exposed to a 6-month light cycle (Lindsay *et al.*, 1984). There is therefore a clear decrease in the magnitude of LH and testosterone changes when the period is as short as 2 months.

Most importantly, these results suggest that, in animals exposed to light cycles with a short period, LH pulsatility is sufficient to maintain testicular weight close to its maximum. Furthermore, in the apparent absence of overstimulation of testosterone release, it is likely that there is no strong feedback effect exerted at the level of the hypothalamo-hypophysial system and effectively no regression of the testicular weight occurs. To date, no major decline of testicular weight has been observed in animals kept under a 2-month light cycle for about 2 years. Finally, the efficiency of the



**Fig. 5.** Variations in testicular weight (mean  $\pm$  s.e.m.) in rams ( $N = 6$ ) exposed to short light cycles (period = 2 months) in which the total daylength (---) is: (a) 8 h given in two blocks, one of 7 h and one of 1 h, and the interval between the initial dawn and the second dusk varies from 8 to 16 h (as in Fig. 2b); (b) short days (8 h) and long days (16 h) alternating every month; and (c) total daylength is 8 h but every other month the 8th hour is given 15–16 h after the initial dawn.

short light cycles in the maintenance of constant sexual activity in the Ile-de-France ram was ascertained by measurement of different sperm values: the volume, concentration and the number of spermatozoa per ejaculate were quite high, at levels characteristic of the sexual season (G. Almeida, G. Touré, G. Colas, Y. Guérin & J. Pelletier, unpublished data).

Because short light cycles are not easy to use from a practical point of view for farmers, other light schedules have been developed.

*Testicular maintenance by a combination of short light cycles and light pulses.* Three parallel experiments are presented in Fig. 5 for 3 groups of 6 Ile-de-France rams.

(a) Light was given in two blocks, one of 7 h and one of 1 h so that the interval between the first 'dawn' and the final 'dusk' varied from 8 to 16 h in 1 month and from 16 to 8 h in the next month. The light schedule was therefore similar to that of the previous experiment (see Fig. 2b) except that the period was 2 months.

(b) The period was also 2 months but short days (8 h) and long days (16 h) were alternated every month.

(c) 'Short' days (8 h) were alternated with 'long' days provided by 2 blocks of light, one of 7 h and a pulse of 1 h given 15–16 h after 'dawn'.

In the three groups of rams testicular weight variations occurred in three phases: (i) there was no change during the 2–3 first months corresponding to the previous natural photorefractory phase since the experiment began in January; (ii) during the next 2–3 months there was a regular increase close to maximum values; and (iii) there were steady high values for the next 5 light cycles, with a tendency for the maximum to rise as the animals, still young (2.5 years old), increased in age.

These different results confirm that testicular weight is maintained when rams are exposed to short light cycles and that 'seasonal' regression is abolished under these conditions. Furthermore, as shown previously with the 6-month light cycles, there is no difference in the patterns of testicular weight if light is provided in one or two blocks. In particular, a light pulse given 15–16 h after 'dawn' can mimic long days. Finally, in these short light cycles, there is no difference in testicular weights when the daylength changes are progressive or when the switches are abrupt.

From a practical point of view the alternation of long and short days every month is easier to apply than the daily adjustment of daylength. Similarly, the use of light pulses can provide 'long' days and save energy, particularly in winter.

### Conclusions

Seasonal reproduction in sheep breeds indigenous to mid-latitudes is detrimental to productivity. These breeds which have a long period of selection usually have particularly interesting traits and cannot be replaced easily. We have developed, therefore, a new light regimen which effectively prevents male seasonal quiescence. It is based on a working hypothesis according to which at least the early photorefractory stage is mainly dependent on gonadal steroids. Indeed, multiplying the number of light stimulations by short applications of decreasing daylength is able to moderate the amplitude of cyclic hypothalamo-hypophysial activity as suggested by the minor variations of the LH and testosterone releases. However, these cyclic changes are such that they allow gametogenesis to be maintained at the highest level without producing testosterone values at which feedback is strongly inhibitory. The use of light pulses makes our schedule a practical possibility. The next step, at present being investigated, is to verify that rams kept in natural daylength (i.e. kept in normal sheep-folds and not in a light-proof building) and exposed each day for 30 days in a 2-month period to a light pulse corresponding to the time of the summer solstice dusk, are able to maintain their full activity all the year round as they do under successive 2-month light cycles. Finally it is expected that repeated 'long days' will prevent photorefractoriness in late autumn. It is also possible that switches from 'long days' to natural daylength will be able to stimulate LH release in winter or early spring and thus to maintain the testicular weight. The mechanism probably involves changes in melatonin secretion (see Bittman & Karsch, 1984) and will be examined.

The measurement of a long day when a light pulse is given 15–16 h after dawn is not limited to Ile-de-France rams: in the ewe such a treatment is also interpreted as a long day. The work of J. Thimonier (unpublished data) offers an interesting alternative to the use of short light cycles since the alternation of long days and short days is provided by the alternation of light pulse treatment (mimicking long days) with feeding melatonin (mimicking short days) to induce ovarian activity at the anticipated time.

In summary, we have transformed the highly seasonal Ile-de-France ram into a male potentially able to reproduce all the year round.

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