

Control of seasonal reproduction in sheep and goats by light and hormones

J. Thimonier

*I.N.R.A., C.R.A.A.G., Station de Recherches Zootechniques, 97170 Petit-Bourg,
French West Indies*

Summary. Seasonal variations of reproductive ability have been demonstrated in male and female sheep and goats. For the female, there is a distinct breeding season. Whilst there are large breed differences in the duration of the sexual season, oestrous cycles generally start when daylength is decreasing and end when daylength is increasing. In some breeds, ovulation without oestrus occurs during the non-breeding season. Although males are able to mate all the year round, seasonal variations occur in the weight of the testis and seminal vesicles and in the fructose concentration of the seminal vesicles. Sexual behaviour and semen characteristics also show seasonal variations.

These seasonal variations in males and females are related to hormonal levels. FSH and LH concentrations in the pituitary are reduced to 50% during the non-breeding season. In the peripheral blood, LH concentrations vary throughout the year whilst prolactin concentrations follow the pattern of daylength. Steroid hormones and their feedback actions at the hypothalamo-pituitary axis play a role in the regulation of seasonal reproduction.

Three different ways are proposed to overcome these seasonal variations. (1) Males can be introduced into a flock of females before the onset of the breeding season. This leads to induction of ovulation and oestrus, although the first ovulation is frequently followed by a short luteal phase. Teasing does not necessitate contact or sight and is only effective after a period of isolation of the females from the males. (2) Oestrus and ovulation may be induced during the anoestrous period by hormonal treatments. Inducers of LH release have to be associated with a progestagen treatment; PMSG is still the most efficient inducer of LH release. Artificial insemination is useful in this context to avoid subfertility due to seasonal variations of the male. (3) The period of reproduction may be controlled by artificial light regimens. There is a photoinducible period in the circadian cycle of the ewe and it may soon be practical to breed out of season by timed exposure of ewes to short periods of light during the normal hours of darkness.

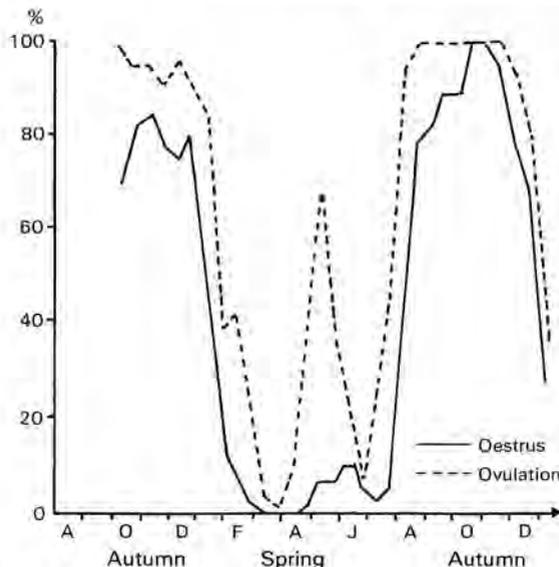
Reproduction in wild animals is often linked to the seasons to ensure that the young are born at a time which maximizes their chance of survival. In domestic animal reproduction, however, seasonality of breeding is a limiting factor because farmers can provide additional food during periods when natural food is short and build shelters to protect the mother and young from the elements. A knowledge of the biological mechanisms determining seasonality is therefore important for the management of domestic sheep and goats.

Seasonality of reproduction in female sheep and goats

Seasonal variations of oestrus and ovulation

In the female, sexual activity is characterized by the occurrence of oestrus but this behaviour cannot be isolated from that of the male. The acceptance of mounting of a female by a male has been generally used to determine the duration of the sexual season. However, this method may be limited by a seasonal change in the libido of the male. The onset and end of the ovulatory period can be determined by following the appearance and disappearance of corpora lutea. This has been done by endoscopy (Thimonier & Mauléon, 1969) or by the determination of plasma levels of progesterone in blood samples collected twice weekly (Thimonier, 1973).

The simultaneous observation of oestrus and ovulation has been made both in the ewe and the goat (Thimonier & Mauléon, 1969; Y. Cognié, personal communication). Ile-de-France and Préalpes du Sud sheep breeds were studied at a latitude of 47°N and Alpine and Criollo goat breeds were studied at a latitude of 16°N. A clear sexual season was observed in all cases (Text-fig. 1) although there were large breed differences. The anoestrous period was longer for Ile-de-France than for Préalpes du Sud sheep (185 days *versus* 100 days) and the Alpine goat had a longer anoestrous period than did the Criollo (230 days *versus* 93 days). Some of the Préalpes du Sud ewes and the Criollo goats showed overt oestrous cycles all year round. These two studies confirm the reports reviewed by Ortavant, Mauléon & Thibault (1964) and the observations of others (Land, Pelletier, Thimonier & Mauléon, 1973; Bindon & Piper, 1976; Wheeler & Land, 1977). The very short sexual season of the Alpine goat resembles that of the Angora goat in South Africa (Pretorius, 1973). For both species, there is a dissociation between oestrus and ovulation. For Ile-de-France and Préalpes du Sud ewes and for the Alpine goat, silent ovulations precede or follow the sexual season. Curiously, for the Criollo goat, the reverse is observed: oestrous cycles, some of short duration, occur without ovulation.



Text-fig. 1. Seasonal variations in the frequency of oestrus and ovulation in Ile-de-France ewes at a latitude of 47°N.

For several breeds, silent ovulations during the anoestrous period are not associated with regular sexual activity (Thimonier & Mauléon, 1969; Land *et al.*, 1973; Wheeler & Land, 1977) and such silent ovulations appear to occur when daylength is increasing. Furthermore, cyclic

ovarian function and oestrous activities start for some females before the longest day which rather contradicts the hypothesis of Yeates (1949) which implies that decreasing daylength governs the onset of reproductive activity in sheep.

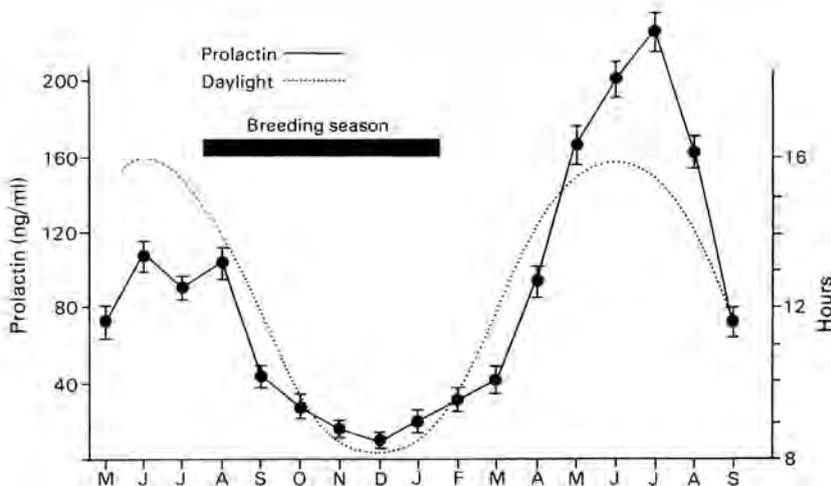
Seasonal variations in hormone production

In the ewe, during the anoestrous period the concentrations of pituitary FSH and LH are 50% of those on Day 12 of the oestrous cycle, when the concentrations are at their maximum (Robertson & Hutchinson, 1962; Thimonier & Mauléon, 1969). According to Pretorius (1974), the mean value for FSH in anoestrous goats was substantially lower than the value recorded for the oestrous cycle. Pituitary LH levels during anoestrus were similar to those found during the mid-luteal phase of the oestrous cycle.

Information on hormone levels in peripheral blood is available for the ewe. LH has been shown to be released in a pulsatile pattern, the frequency of LH pulses varying according to the season and the stage of the cycle (Yuthasastrakosol, Palmer & Howland, 1975; Baird, Swanston & Scaramuzzi, 1976; Scaramuzzi & Baird, 1977; Martensz & Scaramuzzi, 1979; Martensz, Scaramuzzi & Van Look, 1979; Terqui, Garnier, de Reviers, Huet & Pelletier, 1980).

A lot of emphasis has been placed upon the control of LH secretion by oestradiol. In the ewe, there is a marked seasonal change in the negative feedback action of oestradiol on tonic LH secretion: the negative feedback of oestradiol increases towards the end of the sexual season leading to anoestrus. It decreases towards the end of the anoestrous period and resumption of oestrous cycles is once again possible (Legan & Karsch, 1979; Karsch, Goodman & Legan, 1980).

For the Ile-de-France ewe, peripheral levels of prolactin reach their maximum in the summer (up to 200 ng/ml) and their minimum in the winter (<10 ng/ml). The first oestrus of the breeding season appears when prolactin is decreasing and cyclic oestrous behaviour ends when prolactin levels are increasing (Text-fig. 2) (Walton, McNeilly, McNeilly & Cunningham, 1977; Thimonier, Ravault & Ortavant, 1978). Prolactin levels are high in the post-partum period and this may contribute to an additional inhibitory effect on the resumption of ovarian activity (Kann & Martinet, 1975).



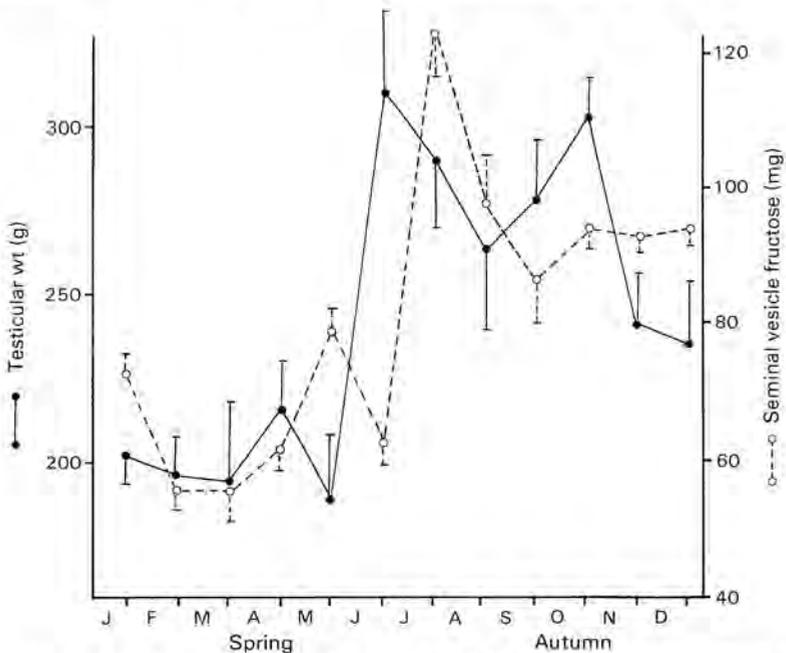
Text-fig. 2. Seasonal variations of prolactin concentrations under normal variations of daylength in Ile-de-France ewes (modified from Thimonier *et al.*, 1978).

For the goat, there is a seasonal variation in the concentration of prolactin released at milking but daylength is the predominant factor governing the autumn decline (Hart, 1975). Low levels of progesterone are observed during anoestrus (Yuthasastrakosol *et al.*, 1975). During the sexual season, the mean concentration of progesterone during the luteal phase is higher in the middle than at the beginning or the end of the season; this phenomenon is not related to the ovulation rate (Lamond, Gaddy & Kennedy, 1972; Wheeler & Land, 1977).

Seasonal reproduction in male sheep and goats

Testis size

Testicular weight in the ram follows a marked seasonal variation (Text-fig. 3). For the Ile-de-France breed, the mean testicular weight is close to 210 g from January to the end of May and increases to a mean value of 285 g (+35%) by the end of October (Pelletier & Ortavant, 1967). In this study two points are worth noting: (1) the rapid increase in testicular weight commences before the longest day, and (2) the decrease in testicular weight occurs before the shortest day. The variation in testicular weight parallels a similar change in the average number of germ cells in a cross-section of a seminiferous tubule. The epididymal sperm reserves undergo a similar variation but with a delay which relates to the time course of sperm production. The increase in weight of the seminal vesicles and their fructose content is rapid between June and July, i.e. 1 month after testicular weight begins to increase (Text-fig. 3).



Text-fig. 3. Seasonal variations of testicular weight and fructose content of seminal vesicles in Ile-de-France rams at a latitude of 47°N (data from Pelletier & Ortavant, 1967).

Libido

Seasonal variations are observed in sexual behaviour in rams and billy goats (Land, 1970; Corteel, 1973) and there are breed differences. Finnish Landrace rams have a higher libido than do Scottish Blackface males but both respond to seasonal change in the same way (Land, 1970).

Libido is not a limiting factor for semen collection with well trained rams or billy goats (Corteel, 1977) although it can be when males are used for the natural breeding of females brought into oestrus out of season.

Seasonal variations in semen characteristics and sperm production

The frequency of semen collections influences the concentration of spermatozoa in the ejaculate and the total number per ejaculate (Colas, Personnic, Courot & Ortavant, 1975). With twice weekly semen collections, seasonal variations in volume and sperm concentration are observed in the billy goat. The volume is three times higher in autumn and winter than in spring. Sperm concentration varies from nearly 7×10^9 spermatozoa/ml in spring and early summer to less than 4×10^9 /ml in winter (Corteel, 1977). In the Ile-de-France rams with the same frequency of semen collections, the quantity of spermatozoa collected varies from 12.8×10^9 spermatozoa/week in April–June to 22.7×10^9 /week in September–November (Colas & Guerin, 1979). Furthermore, in rams (Colas & Courot, 1977), the fertilizing ability is significantly higher in 'autumn' than in 'spring' (63.5 and 50.6% respectively; $0.01 < P < 0.02$) although the mean motility of ejaculates taken at random and used in artificial insemination was the same for both periods. Semen motility is at its highest during autumn in Alpine and Poitevine billy goats (Corteel, 1977).

Seasonal variations in hormone production

For the ram, pituitary concentration and content of LH is approximately twice as high during the period between June and November than from the end of December to May. For FSH, two periods of high activity are observed, one in July and the second in February. There is, however, no increase in spermatogenic activity in the ram in February (Pelletier & Ortavant, 1967).

Early studies with blood samples collected weekly or fortnightly revealed seasonal variation in LH and testosterone levels in the peripheral blood of rams and billy goats (Saumande & Rouger, 1972; Pelletier & Ortavant, 1975). For example, in the Alpine billy goat, an increase in the testosterone levels occurred approximately 45 days after the longest day, and began to decrease again before the shortest day. A similar pattern was observed in the ram. Other studies have shown that LH and testosterone are released in a pulsatile manner (Bolt, 1971; Sanford, Winter, Palmer & Howland, 1974; Muduuli, Sanford, Palmer & Howland, 1979). Each peak of LH is followed after about 1 h by a peak in testosterone (Lincoln, 1976; Wilson & Lapwood, 1978; Terqui *et al.*, 1980). Such a relationship may not always be obvious in the male pygmy goat (Muduuli *et al.*, 1979).

In the ram, the mean LH testosterone values (based on 25 consecutive hourly blood samples) increased from the non-breeding to the breeding season (J. Pelletier, D. H. Garnier, M. M. de Reviers, M. Terqui & R. Ortavant, personal communication), but there are marked differences between breeds. The increase in the mean levels is related mainly to the increase in the number of LH and testosterone peaks (Ravault, Blanc, Ortavant, Pelletier & de Reviers, 1980). LH and testosterone peaks are equally distributed between the light and dark phases. However, the number of LH peaks per 3 h is low just after dawn and increases in the next 6 h. It is suggested that dawn could be one of the synchronizers of gonadotrophin release (Ravault *et al.*, 1980; Terqui *et al.*, 1980). Similar variations are observed in the billy goat (Muduuli *et al.*, 1979).

In the ram, during spring and summer, there is a steady rise in the plasma level of FSH, whilst in September there is a sharp decline (Sanford, Palmer & Howland, 1977; Ravault *et al.*, 1980). A rise in FSH is also observed during the spring in the billy goat (Muduuli *et al.*, 1979). FSH concentrations in the blood do not display pulsatile changes (Ravault *et al.*, 1980).

Finally, prolactin in both species shows a seasonal variation, the highest levels being reached in summer and the lowest during winter (Buttle, 1974; Ravault & Ortavant, 1977; Muduuli *et al.*,

1979; Ravault *et al.*, 1980). A marked diurnal cycle, with maximum secretion of prolactin being observed at night, has been described for the ram (Ravault & Ortavant, 1977; Ravault *et al.*, 1980).

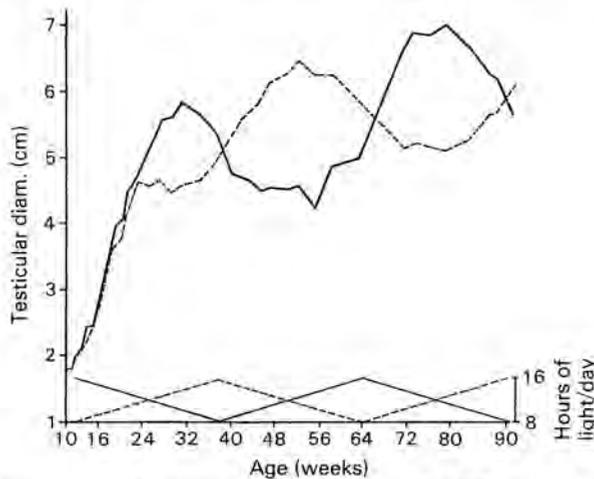
Control of reproduction

From the previous discussion, it is apparent that there is a parallel seasonal variation in the ability to mate and reproduce in the male and female. Since the comprehensive study of Yeates (1949), it has become accepted that the main factor controlling the seasonal nature of breeding activity is daylength. Until recently sheep and goats have been classed as 'short day' animals by contrast to other species which become reproductively active when daylength is increasing (horses, donkeys). However, other environmental factors may be implicated.

In this report, the control of reproduction will be considered only in terms of photoperiod, the interactions between the sexes and hormonal treatment.

Control of reproduction by light

Male. As early as 1956, Ortavant & Thibault, using a 6-month sinusoidal light cycle, obtained high spermatogenic activity under decreasing daylengths, and *vice versa*, thus inducing two seasons of sexual activity per year. Albério & Colas (1976), using a reversed annual variation in daylength, showed that testis growth was reversed (Text-fig. 4) and testes increased in size when daylength was decreasing. Furthermore, as already observed under natural lighting conditions, LH and testosterone levels were higher with decreasing photoperiods.



Text-fig. 4. Variations of testis diameter of rams housed under different lighting schedules (data from Albério & Colas, 1976).

An effect of photoperiod on spermatogenesis is also indicated by the work of Schanbacher & Ford (1979). 'Short-day' rams have testes weighing 45% more than testes from rams exposed to long days. Sperm production in short-day rams (12.9×10^9 spermatozoa/day) is twice that of long-day rams (6.5×10^9 /day). Long days exert deleterious effects on several steps on spermatogenesis. Gonadotrophins are probably involved; both serum LH and FSH levels increase in rams exposed to artificially decreasing daylengths (Lincoln, Peet & Cunningham, 1977). There is by now enough information on the effects of light on hormonal activity, sexual

behaviour and sperm production to suggest that rams can be treated with light to produce semen for artificial insemination in the spring. The displacement of the sexual activity is obtained by a reversal of the annual changes in photoperiod. The quantity and quality of the semen are then comparable to those of semen normally obtained in autumn.

Female. When the annual photoperiod is reversed the sexual seasons are similarly reversed. This phenomenon has been demonstrated by the transport of ewes from the northern to the southern hemisphere and by the application of reversed photoperiods (Yeates, 1949). Several studies have clearly shown that decreasing daylength controls the date of onset of oestrus (Ducker, Thwaites & Bowman, 1970) and that increasing daylength (Ducker & Bowman, 1970a) controls the onset of anoestrus. Furthermore, the greater the decrease (or the increase) in daylength, the sooner the change in sexual activity. The interval between the beginning of the light treatment and the oestrous response depends also on the time of the year, on the previous light treatment and on the breed (Ducker & Bowman, 1970b).

Ewes subjected to an artificial 6-month photoperiodic rhythm exhibit two periods of sexual activity each year (Mauléon & Rougeot, 1962). Curiously, the sexual season under these conditions starts when daylength is increasing and ends when daylength is decreasing. This may be due to the time-lag between light stimulation and the onset of reproduction. Rougeot (1969) demonstrated that the Corsican Mouflon, a marked seasonal breeder, when kept on a 6-month photoperiodic cycle would often lamb twice a year. The average duration of post-partum anoestrus was reduced to 45 days. The shortest time interval between matings was 6.5 months. Early weaning of lambs could allow further reduction of this interval. The application of a reversed seasonal photoperiod in winter allows matings 6–10 weeks after lambing in the following spring. The light treatment has to be applied during pregnancy because of the long time-lag involved (Ducker & Bowman, 1972).

New trends in photoperiodic control of reproduction

For photoperiodic treatments to be efficient there is a need to have either light-proofed buildings or to supply additional illumination; both solutions are expensive. So studies have been designed to obtain basic knowledge of the mechanism of light action in order to eliminate such expense. Different hypotheses have been advanced as to how the brain measures the daily variation in illumination. One of them is based upon an endogenous circadian rhythm of photosensitivity with two distinct periods: during the first part, the organism is "light insensitive" and during the second part, it is "light sensitive" (Bunning, 1960). Thus, the effect of a particular light-dark cycle depends on the timing of the light change relative to the circadian rhythm of photosensitivity. To determine if such a hypothesis was valid for sheep, a group of workers at the Station de Physiologie de la Reproduction, Nouzilly, France, used a so-called "scoto-phase scan" experiment in the ram and in the ewe. Animals pre-conditioned in short or in long photoperiods received 8 h illumination split into two periods of 7 h and 1 h duration. The beginning of the 7 h period was considered to be dawn and the extra hour of light was given at various times during the dark period (Ravault & Ortavant, 1977; Ortavant, Pelletier, Ravault & Thimonier, 1978; Thimonier *et al.*, 1978).

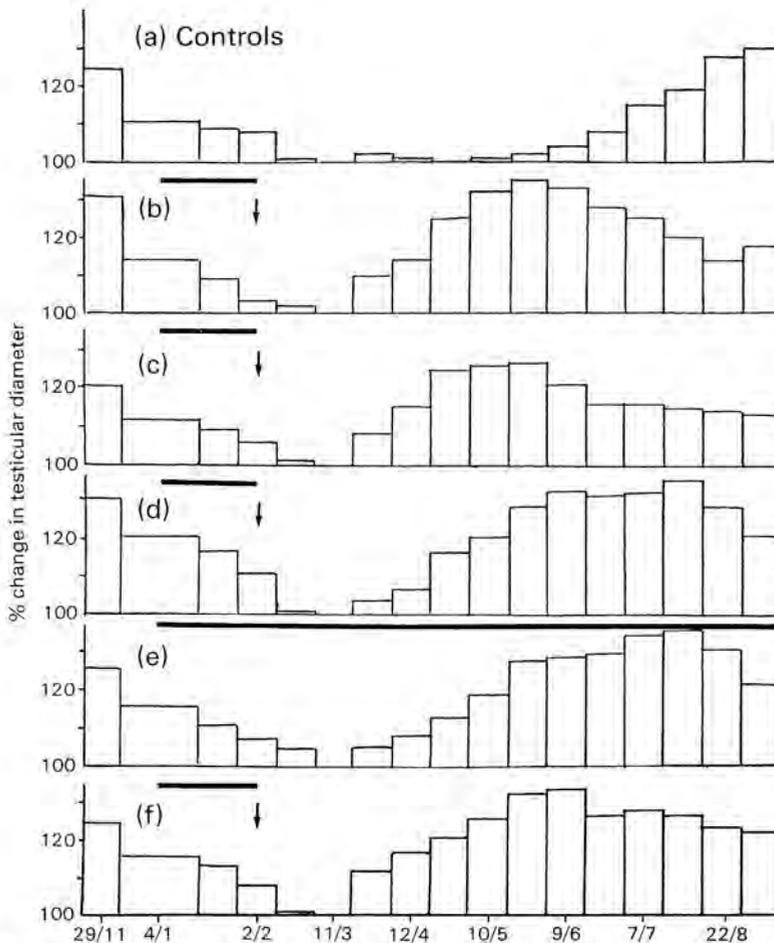
An analysis of progesterone and prolactin levels in ewes subjected for 15 months to these light treatments provided three points of interest: (1) the 1-h light pulse given during the 17th hour after dawn caused a general rise in prolactin; (2) ewes maintained in this constant photoperiod still displayed seasonal changes in prolactin and seasonal variations of temperature may have been responsible for these changes; and (3) high prolactin levels did not inhibit the resumption of ovarian activity.

Blood samples were collected hourly from rams during a 24-h period at different times after the onset of treatment and concentrations of testosterone, LH, FSH and prolactin were measured. The diameter of the testes was measured. The results were as follows: (1) a 1-h light

pulse given during the 17th hour after dawn caused a rise in prolactin; (2) LH secretion increased when the light pulse was given between 11 and 17-h after dawn; and (3) a 1-h light pulse given during the 17th hour after dawn stimulated the growth of the testes.

The reproductive processes of the female and the male therefore appear to contain a photoinducible phase.

As we have already seen with studies of the ewe, the onset of sexual activity is more readily promoted when the light is decreased quickly. So after having primed rams for 1 month and ewes for 3 months with a light pulse during the 17th hour after dawn, one group remained in this light schedule while other groups were formed for which the position of the light pulse was changed to occur during the 8th, 11th, 14th or the 20th hour after dawn.



Text-fig. 5. Variations in testis diameter of rams after a change in the position of the 1-h light pulse in relation to the dawn. (a) The control rams were exposed to normal variation in daylength. Rams in the other groups received a priming light treatment (horizontal bar) for 1 month of 7L:9D:1L:7D with the 1-h light pulse at the 17th hour. Treatments were then changed (arrow) to alter the time of the light pulse: (b) 7L:1L:16D (8th hour); (c) 7L:3D:1L:13D (11th hour); (d) 7L:6D:1L:10D (14th hour); (e) 7L:9D:1L:7D (priming schedule continued, 17th hour); (f) 7L:12D:1L:4D (20th hour). For each group, the value of 100 was given for the lowest mean testis diameter on 11 March. There were 6 rams/group. Data from R. Ortavant, personal communication.

In rams, the priming light pulse was applied when testis diameter was decreasing. After testicular regression, the change in the position of the light pulse was followed in all the groups by an induction of testis growth. The induction was more rapid when the light pulse was given during the 8th or the 11th hour, but the maximum testis diameter was maintained for a longer period in the groups for which the light pulse was given during the 14th hour or maintained during the 17th hour (Text-fig. 5). A similar pattern was observed for the mean 24-h concentrations of FSH and LH measured at different intervals after the beginning of the light treatments (M. R. Blanc & J. Pelletier, personal communication).

For ewes, the priming light pulse (17th hour after dawn) induced a quicker onset of anoestrus than the normal variation in daylength (Table 1). The change in the position of the light pulse induced an earlier subsequent onset of ovarian activity when the light pulse was given during the 8th, 11th or 14th hour. Irregular ovarian cyclicity was observed in groups for which the light pulse was maintained at the 17th hour or given during the 20th hour. These treatments were able to advance the period of ovarian activity by approximately 5 months compared to that in the controls (Table 1).

Table 1. Effect of a change in the position of the 1-h light pulse relative to dawn in ewes after priming with a light pulse at the 17th hour

Priming period 15 September– 9 January	End of ovarian activity date \pm s.d.	Position of the light pulse after the change (h after dawn)	Onset of ovarian activity	
			No. of females with regular ovarian activity	Date \pm s.d.†
7 h light + 1 h 16–17 h after dawn	18 December \pm 21.1 days	7–8	7/8	^a 28 February \pm 28.5 days
		10–11	7/8	^a 2 March \pm 11.3 days
		13–14	5/8	20 February \pm 8.6 days
		16–17	7/8	^b 9 May \pm 11.7 days
		19–20	4/8	20 April \pm 35.7 days
Control group*	17 January \pm 11.6 days		7/7	^c 6 August \pm 11.1 days

* Normal variations of daylength at 47°N.

† Values with different superscript letters are significantly different at $P < 0.05$.

Interruption of seasonal anoestrus by teasing

The introduction of rams into a flock of ewes during anoestrus is followed by a peak of matings: 80% of the females are mated during the period between the 15th and the 24th day (Prud'hon & Denoy, 1969). Such a phenomenon has also been observed in the goat (Shelton, 1960; Ott, Nelson & Hixon, 1980). This induction of oestrus does not occur when rams are kept permanently with the females; a period of isolation is necessary (Riches & Watson, 1954; Oldham, 1980). Recently, the mechanisms involved in the interruption of seasonal anoestrus or advancement of the breeding season by teasing have been studied in Merino sheep. Within 48 h after the introduction of the rams, nearly all the females have ovulated (Oldham, Martin & Knight, 1979). The induced ovulation is silent and is followed in 50% of the females by an abnormal luteal phase of only 6–7 days (Martin, 1979). Immediately after the beginning of teasing there is a significant increase in the frequency of LH pulses and a preovulatory LH discharge occurs within 36 h (Knight, Peterson & Payne, 1978; Cognié, Poindron & Orgeur, 1978; Oldham *et al.*, 1979). Prolactin does not appear to be involved in the process. Teasing is as effective in ewes with high endogenous levels of prolactin as in females treated with bromocriptine (Cognié *et al.*, 1978).

Rams do not need to be in physical contact with the females to induce ovulation (Watson &

Radford, 1960). Induction of ovulation could be mediated by the sense of smell (Morgan, Arnold & Lindsay, 1972) or could involve a complex of signals (Signoret, 1980).

Furthermore, during oestrus itself, the presence of the male reduces markedly the duration of the sexual receptivity and hastens ovulation by advancing the timing of the ovulatory LH discharge (Lindsay, Cognié, Pelletier & Signoret, 1975). This 'ram effect' is in fact well known by some farmers and has been successfully used for a long time to produce out-of-season breeding.

Hormonal control of reproduction

The problem is not so much to induce oestrus and ovulation but to induce a high fertility. As early as 1945, PMSG was given alone to induce ovulation in the anoestrous ewe (Zavadsky, 1945) but oestrus was obtained in only a small percentage of females. In fact, the priming of the central nervous system by progesterone is necessary to obtain behavioural oestrus at the first ovulation of the breeding season (Robinson, 1959). The data presented by Oldham & Martin (1979) and our own data suggest that during the post-partum anoestrus progesterone acts not only to facilitate subsequent oestrous behaviour but also to produce a cycle of normal duration. However, progestagen treatment (progesterone or progestagens) alone given during the anoestrus does not lead to LH release (Pelletier & Thimonier, 1975)—induction of LH discharge is necessary. In spite of a tremendous number of experiments with oestrogens and releasing factors to improve LH release at the end of a progestagen treatment, PMSG has remained the most efficient tool for induction of oestrus and ovulation during anoestrus (Thimonier, 1979) although the interval between onset of oestrus and ovulation is shortened in 20% of the females (Cognié, Mariana & Thimonier, 1970). Teasing in progestagen-primed ewes can successfully induce oestrus and ovulation in the absence of stimulation by PMSG (Cognié, Gayerie, Oldham & Poindron, 1980). However, more information is necessary to specify the response of seasonally anovulatory ewes to teasing after progestagen priming.

Several progestagens have been examined for the control of oestrus and ovulation in the ewe and in the goat, and several routes of administration have been explored. The time to oestrus is variable depending upon the half-life of the progestagen used, the dose given, the route of administration, the duration of treatment, the time of injection, dose of PMSG and the breed (Corteel, 1975).

In fact, the most important problem to be solved with hormonal induction of oestrus and ovulation during anoestrus is the problem of insemination because seasonal variations are well-marked in rams and billy goats. Hormonal treatments to increase sperm production and libido in males have been unsuccessful. Using natural service as the method of breeding needs a ram to ewe ratio of 1 to 5 or 1 to 10 (Gordon, 1975). Prud'hon, Galindez & Reboul (1975) have shown that a ratio of 1 to 48 gave a fertility higher than 88%, but this method leads to a wide range in the time of lambings.

The use of progestagens to control oestrus and ovulation in sheep and goats cannot be dissociated from artificial insemination (Colas, 1975; Corteel, 1975). It was demonstrated by Quinlivan & Robinson (1967, 1969) that progestagens disturb transport and survival of spermatozoa in the female genital tract. The problem of subfertility is now being overcome (Corteel, 1977; Colas, 1979) in several ways. (1) Sperm production in the ram (18 month old) is increased by 20% if training is started at 4–7 months of age. (2) Improvements are being made in the technology for the handling of ram and billy goat semen. For example, temperature, concentration and diluent are important factors with fresh semen. Removal of the seminal plasma from the spermatozoa from the billy goat before dilution and freezing improves subsequent sperm motility and survival and improved fertility results are obtained. (3) It is necessary to have a high selection rate of males for semen quality. (4) The precise timing of artificial insemination in relation to the end of progestagen treatment is important.

Finally, light treatment has been used in combination with progestagens to overcome anoestrus (Robinson, Fraser & McHattie, 1975) and an average production of 3.5 lambs per ewe per year has been obtained from highly prolific crossbred ewes.

References

- Alberio, R. & Colas, G. (1976) Influence of photoperiodism on the sexual development of the young Ile de France ram. *Proc. 8th Int. Congr. Anim. Reprod. & A.I., Krakow*, 3, 26–29.
- Baird, D.T., Swanston, I. & Scaramuzzi, R.J. (1976) Pulsatile release of LH and secretion of ovarian steroids in sheep during the luteal-phase of the estrus cycle. *Endocrinology* 98, 1490–1496.
- Bindon, B.M. & Piper, L.R. (1976) Assessment of new and traditional techniques of selection for reproduction rate. In *Sheep Breeding; Proceedings of the 1976 International Congress, Muresk and Perth*, pp. 357–370. Eds G. E. Tomes, D. E. Robertson & R. J. Lightfoot, Western Australian Institute of Technology, Perth.
- Bolt, D.J. (1971) Changes in the concentration of luteinizing hormone in plasma of rams following administration of oestradiol, progesterone or testosterone. *J. Reprod. Fert.* 24, 435–438.
- Bunning, E. (1960) Circadian rhythms and the time measurement in photoperiodism. In *Biological Clocks. Cold Spring Harbor. Symp. Quant. Biol.* 25, 249–256.
- Buttle, H.L. (1974) Seasonal variation of prolactin in plasma of male goats. *J. Reprod. Fert.* 37, 95–99.
- Cognié, Y., Mariana, J.C. & Thimonier, J. (1970) Etude du moment d'ovulation chez la brebis normale ou traitée par un progestagène associé ou non à une injection de PMSG. *Annls Biol. anim. Biochim. Biophys.* 10, 15–24.
- Cognié, Y., Poindron, P. & Orgeur, P. (1978) Rupture de la période de repos sexuel saisonnier chez la brebis par l'effet bélier et le blocage de la sécrétion de prolactine. *Journées (4th) de la Recherche Ovine et Caprine; I.N.R.A.-I.T.O.V.I.C.* pp. 339–349.
- Cognié, Y., Gayerie, F., Oldham, C.M. & Poindron, P. (1980) Increased ovulation rate at the ram-induced ovulation and its commercial application. *Proc. Aust. Soc. Anim. Prod.* 13, 80–86.
- Colas, G. (1975) The use of progestagen SC 9880 as an aid for artificial insemination in ewes. *Annls Biol. anim. Biochim. Biophys.* 15, 317–327.
- Colas, G. (1979) Fertility in the ewe after artificial insemination with fresh and frozen semen at the induced oestrus and influence of the photoperiod on the semen quality of the ram. *Livestock Production Science* 6, 153–166.
- Colas, G. & Courot, M. (1977) Production of spermatozoa, storage of semen and artificial insemination in the sheep. In *Management of Reproduction in Sheep and Goats*, pp. 31–40. University of Wisconsin, Madison.
- Colas, G. & Guerin, Y. (1979) L'insémination artificielle chez les ovins: acquisitions et perspectives. *Journées (5th) de la Recherche Ovine et Caprine; I.N.R.A.-I.T.O.V.I.C.* pp. 162–185.
- Colas, G., Personnic, D., Courot, M. & Ortavant, R. (1975) Influence du rythme de collecte sur la production de spermatozoïdes chez le jeune bélier Romanov. *Ann. Zootech.* 24, 189–198.
- Corteel, J.M. (1973) L'insémination artificielle caprine: bases physiologiques, état actuel et perspectives d'avenir. *World Rev. Anim. Prod.* 9, 73–99.
- Corteel, J.M. (1975) The use of progestagens to control the oestrous cycle of the dairy goat. *Annls Biol. anim. Biochim. Biophys.* 15, 353–363.
- Corteel, J.M. (1977) Production, storage and insemination of goat semen. In *Management of Reproduction in Sheep and Goats*, pp. 41–57. University of Wisconsin, Madison.
- Ducker, M.J. & Bowman, J.C. (1970a) Photoperiodism in the ewe. 3. The effects of various patterns of increasing daylength on the onset of anoestrus in Clun-Forest ewes. *Anim. Prod.* 12, 465–471.
- Ducker, M.J. & Bowman, J.C. (1970b) Photoperiodism in the ewe. 4. A note on the effect on onset of oestrus in Clun-Forest ewes of applying the same decrease in daylength at two different times of the year. *Anim. Prod.* 12, 513–516.
- Ducker, M.J. & Bowman, J.C. (1972) Photoperiodism in the ewe. 5. An attempt to induce sheep of three breeds to lamb every eight months by artificial daylength changes in a non-light-proofed building. *Anim. Prod.* 14, 323–334.
- Ducker, M.J., Thwaites, C.J. & Bowman, J.C. (1970) Photoperiodism in the ewe. 2. The effects various patterns of decreasing daylength on the onset of oestrus in Clun-Forest ewes. *Anim. Prod.* 12, 115–123.
- Gordon, I. (1975) The use of progestagens in sheep bred by natural and artificial insemination. *Annls Biol. anim. Biochim. Biophys.* 15, 303–315.
- Hart, I.C. (1975) Seasonal factors affecting the release of prolactin in goats in response to milking. *J. Endocr.* 64, 313–322.
- Kann, G. & Martinet, J. (1975) Prolactin levels and duration of post-partum anoestrus in lactating ewes. *Nature, Lond.* 257, 63–64.
- Karsch, F.J., Goodman, R.L. & Legan, S.J. (1980) Feedback basis of seasonal breeding: test of an hypothesis. *J. Reprod. Fert.* 58, 521–535.
- Knight, T.W., Peterson, A.J. & Payne, E. (1978) The ovarian and hormonal response of the ewe to stimulation by the ram early in the breeding season. *Theriogenology* 10, 343–353.
- Lamond, D.R., Gaddy, R.G. & Kennedy, S.W. (1972) Influence of season and nutrition on luteal plasma progesterone in Rambouillet ewes. *J. Anim. Sci.* 34, 626–629.
- Land, R.B. (1970) The mating behaviour and semen characteristics of Finnish Landrace and Scottish Blackface rams. *Anim. Prod.* 12, 551–560.

- Land, R.B., Pelletier, J., Thimonier, J. & Mauléon, P. (1973) A quantitative study of genetic differences in the incidence of oestrus, ovulation and plasma luteinizing hormone concentration in the sheep. *J. Endocr.* **58**, 305–317.
- Legan, S.J. & Karsch, F.J. (1979) Neuroendocrine regulation of the estrus cycle and seasonal breeding in the ewe. *Biol. Reprod.* **20**, 74–85.
- Lincoln, G.A. (1976) Seasonal variation in the episodic secretion of luteinizing hormone and testosterone in rams. *J. Endocr.* **69**, 213–226.
- Lincoln, G.A., Peet, M.J. & Cunningham, R.A. (1977) Seasonal and circadian changes in the episodic release of FSH, LH and testosterone in rams exposed to artificial photoperiods. *J. Endocr.* **72**, 337–349.
- Lindsay, D.R., Cognié, Y., Pelletier, J. & Signoret, J.P. (1975) Influence of the presence of rams on the timing of ovulation and discharge of LH in ewes. *Physiol. Behav.* **15**, 423–426.
- Martensz, N.D. & Scaramuzzi, R.J. (1979) Plasma concentrations of luteinizing hormone, follicle-stimulating hormone and progesterone during the breeding season in ewes immunized against androstenedione or testosterone. *J. Endocr.* **81**, 249–259.
- Martensz, N.D., Scaramuzzi, R.J. & Van Look, P.F.A. (1979) Plasma concentrations of luteinizing hormone and follicle-stimulating hormone during anoestrus in ewes actively immunized against oestradiol-17 β , oestrone or testosterone. *J. Endocr.* **81**, 261–269.
- Martin, G.B. (1979) Ram-induced ovulation in seasonally anovular Merino ewes: effect of estradiol on the frequency of ovulation, estrus and short cycles. *Theriogenology* **12**, 283–287.
- Mauléon, P. & Rougeot, J. (1962) Régulation des saisons sexuelles chez des brebis de races différentes au moyen de divers rythmes lumineux. *Annls Biol. anim. Biochim. Biophys.* **2**, 209–222.
- Morgan, P.D., Arnold, G.W. & Lindsay, D.R. (1972) A note on the mating behaviour of ewes with various senses impaired. *J. Reprod. Fert.* **30**, 151–152.
- Muduuli, D.S., Sanford, L.M., Palmer, W.M. & Howland, B.E. (1979) Secretory patterns and circadian and seasonal changes in luteinizing hormone, follicle stimulating hormone, prolactin and testosterone in the male pygmy goat. *J. Anim. Sci.* **49**, 543–553.
- Oldham, C.M. (1980) Stimulation of ovulation in seasonally or lactationally anovular ewes by rams. *Proc. Aust. Soc. Anim. Prod.* **13**, 73–76.
- Oldham, C.M. & Martin, G.B. (1979) Stimulation of seasonally anovular Merino ewes by rams. II. Premature regression of ram-induced corpora lutea. *Anim. Reprod. Sci.* **1**, 291–295.
- Oldham, C.M., Martin, G.B. & Knight, T.W. (1979) Stimulation of seasonally anovular Merino ewes by rams. I. Time from introduction of the rams to the preovulatory LH surge and ovulation. *Anim. Reprod. Sci.* **1**, 283–290.
- Ortavant, R. & Thibault, C. (1956) Influence de la durée d'éclaircissement sur les productions spermatiques du bélier. *C.r. Séanc. Soc. Biol.* **150**, 358–361.
- Ortavant, R., Mauléon, P. & Thibault, C. (1964) Photoperiodic control of gonadal and hypophyseal activity in domestic mammals. *Ann. N.Y. Acad. Sci.* **117**, 157–193.
- Ortavant, R., Pelletier, J., Ravault, J.P. & Thimonier, J. (1978) Annual cyclic variations in prolactin in sheep. In *Environmental Endocrinology*, pp. 75–78. Eds I. Assenmacher & D. S. Farner. Springer-Verlag, Berlin.
- Ott, R.S., Nelson, D.R. & Hixon, J.E. (1980) Effect of presence of the male on initiation of estrous cycle activity of goats. *Theriogenology* **13**, 183–190.
- Pelletier, J. & Ortavant, R. (1967) Influence du photopériodisme sur les activités sexuelle, hypophysaire et hypothalamique du bélier Ile de France. In *La photorégulation chez les Oiseaux et les Mammifères*, pp. 483–495. Y. Assenmacher & J. Benoit. C.N.R.S., Paris.
- Pelletier, J. & Ortavant, R. (1975) Photoperiodic control of LH release in the ram. I. Influence of increasing and decreasing light photoperiods. *Acta endocr., Copenh.* **78**, 435–441.
- Pelletier, J. & Thimonier, J. (1975) Interactions between ovarian steroids or progestagens and LH release. *Annls Biol. anim. Biochim. Biophys.* **15**, 131–146.
- Pretorius, P.S. (1973) Cyclic reproductive activity in the Angora goat. *Agroanimalia* **5**, 55–58.
- Pretorius, P.S. (1974) Fluctuations in pituitary FSH and LH in the normally cycling and in the anoestrous Angora Goat. *J. Sth Afr. Vet. Ass.* **45**, 173–176.
- Prud'hon, M. & Denoy, I. (1969) Effets de l'introduction de béliers vasectomisés dans un troupeau Mérinos d'Arles, quinze jours avant le début de la lutte de Printemps, sur l'apparition des oestrus, la fréquence des erreurs de détection des rûts et la fertilité des brebis. *Ann. Zootech.* **18**, 95–106.
- Prud'hon, M., Galindez, F. & Reboul, G. (1975) Induction des oestrus et lutte libre chez les brebis Mérinos d'Arles: influence de la saison, de la lactation et du rapport bélier-brebis sur la fertilité et la prolificité. *Journées (1st) de la Recherche Ovine et Caprine, I.N.R.A.—I.T.O.V.I.C.* **II**, 293–302.
- Quinlivan, T.D. & Robinson, T.J. (1967) The number of spermatozoa in the fallopian tubes of ewes at intervals after artificial insemination following withdrawal of SC 9880 impregnated intravaginal sponges. In *The Control of the Ovarian Cycle in the Sheep*, pp. 177–194. Ed. T. J. Robinson. Sydney University Press.
- Quinlivan, T.D. & Robinson, T.J. (1969) Numbers of spermatozoa in the genital tract after artificial insemination of progestagen treated ewes. *J. Reprod. Fert.* **19**, 73–86.
- Ravault, J.P. & Ortavant, R. (1977) Light control of prolactin secretion in sheep. Evidence for a photo-inducible phase during a diurnal rhythm. *Annls Biol. anim. Biochim. Biophys.* **17**, 459–473.
- Ravault, J.P., Blanc, M., Ortavant, R., Pelletier, J. & de Revières, M.M. (1980) Variations circadiennes et circannuelles de la sécrétion de prolactine (Prl), LH et FSH chez les animaux domestiques mâles. In *Rythmes et Reproduction*, pp. 115–128. Eds R. Ortavant & A. Reinberg. Masson & Cie, Paris.
- Riches, J.M. & Watson, R.M. (1954) The influence of the introduction of rams on the incidence of oestrus in Merino ewes. *Aust. J. agric. Res.* **5**, 141–147.
- Robertson, H.A. & Hutchinson, J.S.M. (1962) The levels of FSH and LH in the pituitary of the ewe in relation to follicular growth and ovulation. *J. Endocr.* **24**, 143–151.

- Robinson, J.J., Fraser, C. & McHattie, I.** (1975) The use of progestagens and photoperiodism in improving the reproductive rate of the ewe. *Annls Biol. anim. Biochim. Biophys.* **15**, 345–352.
- Robinson, T.J.** (1959) The estrous cycle of the ewe and doe. In *Reproduction in Domestic Animals*, 1st edn. Vol. I, pp. 291–333. Eds H. H. Cole & P. T. Cupps. Academic Press, New York.
- Rougeot, J.** (1969) Accélération du rythme de la reproduction chez le Mouflon de Corse (*Ovis ammon musimon*, Schreber, 1782) au moyen de cycles photopériodiques semestriels. *Annls Biol. anim. Biochim. Biophys.* **9**, 441–443.
- Sanford, L.M., Winter, J.S.D., Palmer, W.M. & Howland, B.E.** (1974) The profile of LH and testosterone secretion in the ram. *Endocrinology* **95**, 627–631.
- Sanford, L.M., Palmer, W.M. & Howland, B.E.** (1977) Changes in the profiles of serum LH, FSH and testosterone and in mating performance and ejaculate volume in the ram during the ovine breeding season. *J. Anim. Sci.* **45**, 1382–1391.
- Saumande, J. & Rouger, Y.** (1972) Variations saisonnières des taux d'androgènes dans le plasma périphérique chez le Bouc. *C.r. hebdom. Séanc. Acad. Sci., Paris D* **274**, 89–92.
- Scaramuzzi, R.J. & Baird, D.T.** (1977) Pulsatile release of luteinizing hormone and the secretion of ovarian steroids in sheep during anestrus. *Endocrinology* **101**, 1801–1806.
- Schanbacher, B.D. & Ford, J.J.** (1979) Photoperiodic regulation of ovine spermatogenesis; relationship to serum hormones. *Biol. Reprod.* **20**, 719–726.
- Shelton, M.** (1960) Influence of the presence of a male goat on the initiation of estrous cycles and ovulation of Angora does. *J. Anim. Sci.* **19**, 368–375.
- Signoret, J.P.** (1980) Effet de la présence du mâle sur les mécanismes de reproduction chez la femelle des mammifères. *Reprod. Nutr. Dévelop.* **20**, 457–468.
- Terqui, M., Garnier, D.H., de Reviere, M.M., Huet, S. & Pelletier, J.** (1980) La structure chronologique du dialogue entre l'hypophyse et les gonades chez les mammifères domestiques. In *Rythmes et Reproduction*, pp. 59–72. Eds R. Ortavant & A. Reinberg. Masson & Cie, Paris.
- Thimonier, J.** (1973) Diagnostic précoce de la gestation par l'estimation du taux de progestérone plasmatique chez la brebis, la vache et la jument. *Rec. Med. Vet.* **149**, 1303–1318.
- Thimonier, J.** (1979) Hormonal control of oestrous cycle in the ewe (a review). *Livestock Production Science* **6**, 39–50.
- Thimonier, J. & Mauléon, P.** (1969) Variations saisonnières du comportement d'oestrus et des activités ovarienne et hypophysaire chez les ovins. *Annls Biol. anim. Biochim. Biophys.* **9**, 233–250.
- Thimonier, J., Ravault, J.P. & Ortavant, R.** (1978) Plasma prolactin variations and cyclic ovarian activity in ewes submitted to different light regimens. *Annls Biol. anim. Biochim. Biophys.* **18**, 1229–1235.
- Walton, J.S., McNeilly, J.R., McNeilly, A.S. & Cunningham, F.J.** (1977) Changes in blood levels of prolactin, LH, FSH and progesterone during anoestrus in the ewe. *J. Endocr.* **75**, 127–136.
- Watson, R.H. & Radford, H.M.** (1960) The influence of rams on onset of oestrus in Merino ewes in the spring. *Aust. J. Agric. Res.* **11**, 65–71.
- Wheeler, A.G. & Land, R.B.** (1977) Seasonal variation in oestrus and ovarian activity of Finnish Landrace, Tasmanian Merino and Scottish Blackface ewes. *Anim. Prod.* **24**, 363–376.
- Wilson, P.R. & Lapwood, K.R.** (1978) Studies of hormone secretion in Romney Ram: luteinizing hormone, testosterone and prolactin plasma profiles, LH/testosterone inter-relationships and the influence of seasons. *Theriogenology* **9**, 279–294.
- Yeates, N.T.M.** (1949) The breeding season of the sheep with particular reference to its modification by artificial means using light. *J. agric. Sci., Camb.* **39**, 1–43.
- Yuthasastrakosol, P., Palmer, W.M. & Howland, B.E.** (1975) Luteinizing hormone, oestrogen and progesterone levels in peripheral serum of anoestrous and cyclic ewes as determined by radioimmunoassay. *J. Reprod. Fert.* **43**, 57–65.
- Zavadosky, B.M.** (1945) [Directing the Processes of Reproduction in Animals.] In Russian, Sel'khozgiz, Moscow.