

# Photoperiodic requirements for timing onset and duration of the breeding season of the ewe: Synchronization of an endogenous rhythm of reproduction\*

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**Summary.** A study was conducted to test the hypothesis that different portions of the annual photoperiodic cycle play different roles in timing the breeding season of the ewe, *Ovis aries*, an animal in which an endogenous rhythm generates the seasonal reproductive transitions. Adult female sheep were pinealectomized to disrupt transduction of photoperiodic cues at 4 times of the year (summer and winter solstices, vernal and autumnal equinoxes), and the effects on seasonal reproductive neuroendocrine activity were evaluated. Time of pinealectomy greatly influenced the subsequent seasonal reproductive cycle such that the following inferences are possible. Lengthening days between the winter and summer solstices synchronize reproductive onset to the appropriate time of year. The relatively long days around the summer solstice act to suppress reproductive activity and forestall the start of the breeding season until late summer/early autumn. The shortening days between the summer solstice and autumnal equinox maintain a normal intensity and duration of reproductive neuroendocrine induction during the impending breeding season. However, the shortening days between the autumnal equinox and winter solstice (i.e., after breeding season onset) do not appear to play a critical role in maintaining the breeding season of that year, but may provide important cues for timing the breeding season of the following year.

**Key words:** Circannual rhythm – Photoperiod – Pineal gland – Seasonal breeding

*Abbreviations:* LH luteinizing hormone

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## Introduction

It is well documented in a variety of seasonal breeders that photoperiodic signals play a critical role in timing reproduction. In some species, at least one reproductive transition results from photoperiod acting as a direct-driving force. This is illustrated in the Syrian hamster in which gonadal regression at the end of the breeding season is a direct result of the inhibitory effects of short days (Reiter 1972; Turek et al. 1975). On the other hand, gonadal recrudescence in the spring does not require the inductive effects of long days but results from a loss of responsiveness to short days (Reiter 1972; Turek et al. 1975). Exposure to long days is required to break this photorefractoriness to short day lengths (Reiter 1972; Stetson et al. 1977). This dependence on photoperiodically-driven transitions into and/or out of the breeding season seems to be endemic to short-lived species. In some long-lived species, however, neither reproductive transition is driven by photoperiod; rather, each transition is generated endogenously and reflects a circannual rhythm of reproduction which is entrained by photoperiod (Gwinner 1986). In such animals, it is not clear what the roles of different portions of the annual photoperiod are in timing the reproductive transitions.

The sheep, a long-lived animal, displays annual bouts of reproductive activity which typically begin in late summer/early autumn when day length is decreasing. Exposure to short days during the anestrus season can drive out-of-season breeding in ewes (Fraser and Laing 1969; Ducker and Bowman 1970; Legan and Karsch 1980; Bittman et al. 1983a, b; Kennaway et al. 1983). This has been taken as evidence that shortening days of late summer and autumn stimulate the onset of reproductive activity under natural environmental conditions. Several studies in the ewe, however, have shown that the onset of the natural breeding season may not require a decrease in day length; moreover, termination of the breeding season may not require an increase in day length (Worthy and Haresign 1983; Robinson and Karsch 1984; Robinson et al. 1985a; Worthy et al. 1985). Further, when sheep are held on a fixed photope-

riod, long-term fluctuations in reproductive activity can continue but become desynchronized from both time of year and among individuals (Ducker et al. 1973; Howles et al. 1982; Karsch et al. 1989). These observations suggest the seasonal reproductive cycle of the ewe is generated by an endogenous process – a circannual rhythm that is not driven by photoperiod but which is entrained by it.

Recent studies in the sheep, as well as in photoperiodic rodents, suggest that the direction of change in day length (i.e., photoperiodic history) determines the reproductive response to a given photoperiodic signal (Horton 1984; Hoffmann et al. 1986; Robinson and Karsch 1987; Hastings et al. 1987). For instance, ewes switched from a long to intermediate photoperiod show an inductive response, while ewes switched from a short photoperiod to the same intermediate photoperiod show an inhibitory response (Robinson and Karsch 1987). The photic information that occurs in the animal's past is therefore crucial to timing the breeding season.

In the present study, we tested the hypothesis that different portions of the annual photoperiodic cycle are of differential importance in timing the seasonal reproductive cycle of a species in which both reproductive transitions are generated endogenously. Our approach was to disrupt the photoperiodic timekeeping process of the ewe by pinealectomy at different times of year and to determine the consequences on both the onset and termination of the subsequent breeding season. We predicted that pinealectomy at different times would have differential effects depending on the animal's photoperiodic history prior to pinealectomy and the role normally played by that portion of the photoperiodic cycle following pinealectomy.

## Materials and methods

**General.** Adult ewes, either purebred Suffolk or predominantly Suffolk breed, were kept outdoors at the Sheep Research Facility near Ann Arbor, MI (42°18' north latitude). They were maintained on pasture from late spring to mid-autumn, and fed hay at other times of year. Animals had free access to mineral licks and water.

Pinealectomy was performed by the method of Roche and Dziuk (1969), modified slightly as described by Dempsey et al. (1982). Completeness of pinealectomy was verified initially by visual inspection of the excised pineal gland and site of removal, and subsequently by documentation that the nocturnal rise in melatonin was eliminated (see below). Prior to pinealectomy, all ewes were ovariectomized and implanted s.c. with one Silastic capsule packed with 3.0 cm of estradiol (Karsch et al. 1973). The estradiol capsules are known to maintain a physiological level of serum estradiol for a period exceeding the length of this study (3–5 pg/ml; Legan et al. 1977). Reproductive neuroendocrine activity was assessed by the concentrations of serum luteinizing hormone (LH) in blood samples (5 ml) taken twice weekly by jugular venipuncture. Changes in circulating LH reflect alterations in the hypothalamic response to estradiol negative-feedback, and this constitutes a major neuroendocrine determinant of seasonal reproduction in the ewe (Legan et al. 1977). Rising and falling levels of serum LH are photoperiodically regulated and are coincident with the onset and termination of breeding activity in ovary-intact ewes, respectively. These swings in serum LH are large (>30-fold) and thus provide a highly robust marker of the seasonal reproductive

state (Legan et al. 1977). Times of elevated LH are defined as the 'neuroendocrine breeding season' (see Analysis of data).

**Assays.** Serum was obtained after blood was allowed to clot at 4 °C and stored at –20 °C until assayed. LH was determined in duplicate 25–200 µl aliquots of serum and is expressed as ng NIH-LH-S12 per ml as previously described (Niswender et al. 1968, 1969; Hauger et al. 1977). The intraassay coefficient of variation (CV) for standard sera containing  $0.93 \pm 0.02$  (mean  $\pm$  SEM),  $2.16 \pm 0.03$  and  $30.66 \pm 0.63$  ng/ml LH averaged 6.6%. The interassay CV for the 3 serum pools averaged 8.5%. The limit of detection (2 standard deviations from buffer control) averaged  $0.25 \pm 0.03$  ng/ml for 200 µl of serum. To standardize the baseline for statistical purposes, LH data below 0.44 ng/ml (upper range of limit of detections for all assays in this study) were assigned this value.

To verify the completeness of pinealectomy, melatonin was assayed in duplicate 200 µl aliquots of serum (5 daytime and 5 nighttime blood samples from each ewe) using the method of English et al. (1986), modified as described by Malpoux et al. (1987, 1988). The intraassay CV for standard sera containing  $92.2 \pm 4.6$  and  $427.1 \pm 19.2$  pg/ml averaged 9.1%. The interassay CV for the 2 serum pools averaged 13.4%. The limit of detection was  $14.1 \pm 3.5$  pg/ml for 200 µl serum. The melatonin rhythm was abolished in all pinealectomized ewes (serum melatonin was low to undetectable in both daytime and nighttime samples). Normal nighttime levels usually exceed 200 pg/ml (Malpoux et al. 1987, 1988).

**Experimental design.** The study was conducted over a two year period (June 1986–April 1988). During the first year, ewes were pinealectomized at one of 4 times when they would have had different photoperiodic histories and been in different reproductive states. Six ewes were pinealectomized around the summer solstice (12–23 June 1986); these ewes had experienced the full complement of increasing day lengths and were in the mid-anestrus season. Six ewes were pinealectomized around the autumnal equinox (11 September–1 October 1986); these had experienced some shortening days and were in the transition into the breeding season. Six ewes were pinealectomized around the winter solstice (8–22 December 1986); these had experienced the full complement of shortening day lengths and were in the late breeding season. Six ewes were pinealectomized around the spring equinox (9 March–3 April 1987); these had experienced some lengthening days and were in the early anestrus season. All ewes were maintained with rams and other ewes prior to pinealectomy; thereafter they were physically isolated in a pasture separate from rams and other ewes to minimize social influences on reproductive function. (Spring pinealectomized ewes served as a control in another study; Pinx Isolated group in Wayne et al. 1989). The control group consisted of pineal-intact ewes for determination of the normal seasonal reproductive cycle in each of the two years of the study. This group consisted of 16 ewes from July 1986 to March 1987, when it was reduced to 8 ewes (due to pinealectomy for the spring group). The Control group was maintained with normal rams and ewes throughout the study.

**Analysis of data.** Rises and declines in serum LH were identified by an algorithm that uses regression-like statistics with a moving variable-length window to detect changes in hormone levels (Malpoux et al. 1988), modified as described by Wayne and coworkers (1988). This algorithm can identify 4 phases of a cycle: baseline, rise, plateau, and decline. The LH elevation was defined as the interval between the start of the rising phase and the end of the decline phase of the serum LH profile. The peak level was defined as the mean value during the plateau phase. Differences in mean peak levels were analyzed by a one-way ANOVA and unpaired *t*-test (Brown and Hollander 1977). Differences in the timing of rises and declines of LH and the duration of elevated LH were analyzed by the Kruskal-Wallis test (analysis of variance) and the Mann-Whitney U test (two groups) (Siegel 1956). Values were considered significantly different if  $P < 0.05$ . Due to practical constraints, it was not possible to monitor all groups for the same

length of time following pinealectomy (duration of observations ranged from 1–2 years as indicated in Results).

Because there were occasional periods of elevated LH that were very brief in duration (sometimes lasting only a few days), we chose to distinguish between these bouts of elevated LH and longer periods of elevated LH which may have greater reproductive significance. The criterion to make this distinction was that LH had to be elevated for more than 34 days (duration of two complete estrous cycles in intact ewes) to be considered a 'neuroendocrine breeding season'. The rationale behind this criterion was that the first ovulation of the breeding season is 'silent'; it is not until the second ovulation that behavioral estrus is manifest. Therefore, the opportunity for breeding is not available until the second estrous cycle. Thus, only periods of elevated LH that exceeded 34 days were considered neuroendocrine breeding seasons.

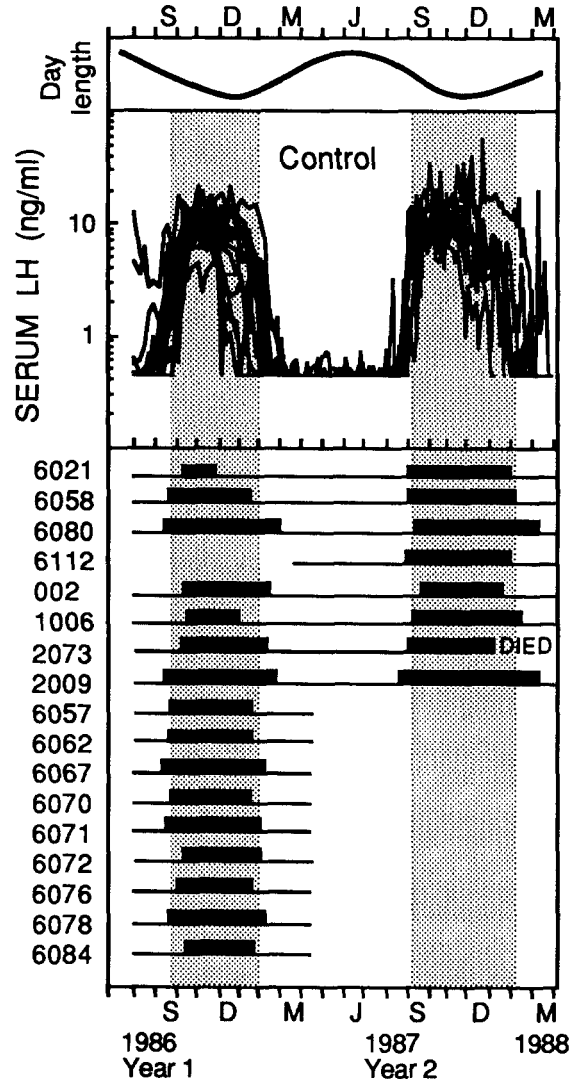
**Results**

Patterns of serum LH are shown in Figs. 1–5. The upper panels show the annual photoperiodic cycle and the times of surgery in pinealectomized ewes; the middle panels show LH values for individual animals; the lower panels show the times of elevated LH for each ewe (identified by the algorithm; see Analysis of data in Methods). The shaded area in all figures represents the mean period of elevated LH in the Control group for comparison. Data summarizing timing, duration and peak LH values for all groups are presented in Table 1.

**Table 1.** Characteristics of the LH elevations during years 1 and 2 of study<sup>a</sup>

	Onset LH rise	End LH elevation	Duration LH elevation (days)	Peak level (ng/ml)
<b>Control</b>				
Year 1	Sept 28 ± 3	Jan 25 ± 7	123 ± 8	9.3 ± 0.7
Year 2	Sept 5 ± 3	Feb 8 ± 7	155 ± 9	9.6 ± 1.5
<b>Summer Px</b>				
Year 1	Aug 10 ± 4**	Oct 28 ± 14**	78 ± 10*	4.7 ± 0.9**
Year 2	b	b	b	b
<b>Autumn Px</b>				
Year 1	(Sept 9 ± 7)	Jan 7 ± 5*	117 ± 7	9.2 ± 1.16
Year 2	b	b	b	b
<b>Winter Px</b>				
Year 1	(Sept 29 ± 6)	Jan 25 ± 7	118 ± 9	8.2 ± 1.54
Year 2	b	b	b	b
<b>Spring Px</b>				
Year 1	c	c	c	c
Year 2	Nov 14 ± 16*	d	d	7.2 ± 0.8

a. values in all columns are mean ± SEM  
 b. not calculated because timing too variable to pool data  
 c. not determined because surgery performed after neuroendocrine breeding season of year 1  
 d. not determined because 5 of 6 ewes failed to show a fall in LH before the end of study  
 ( ) dates not compared to those of Unoperated Controls because surgery performed after onset of LH rise. \* P < 0.05 relative to Control; \*\* P < 0.01 relative to Control



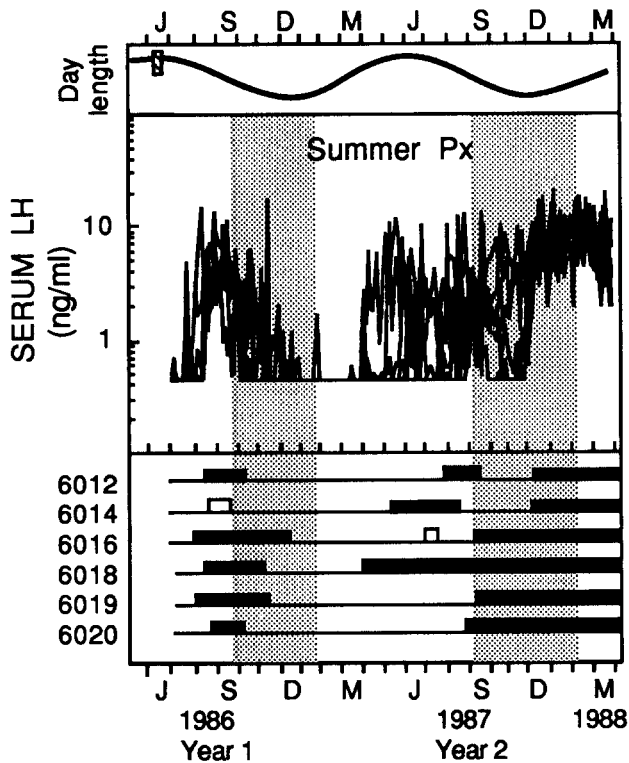
**Fig. 1.** Serum LH patterns in the Control group (pineal-intact). Upper panel: Annual photoperiod curve showing relative changes in day length. Middle panel: Serum LH values for individual ewes plotted on a logarithmic scale. Lower panel: Black bars represent the period of elevated LH for each ewe (see Materials and methods). Thin black lines depict the period of observation for each ewe. Shaded area: mean period of elevated LH in this group. Animal number provided next to data

*Control group (Fig. 1)*

In the Control group, LH levels rose in September, on average, and fell to baseline in January–February in each of the two years of the study. Peak levels of LH reached approximately 10 ng/ml, whereas nadirs were generally undetectable (<0.44 ng/ml). Duration of the LH elevation averaged 123 and 155 days for the two years (Table 1).

*Summer-solstice pinealectomy (Fig. 2)*

The LH rise subsequent to pinealectomy around the summer solstice began in August, earlier than in the

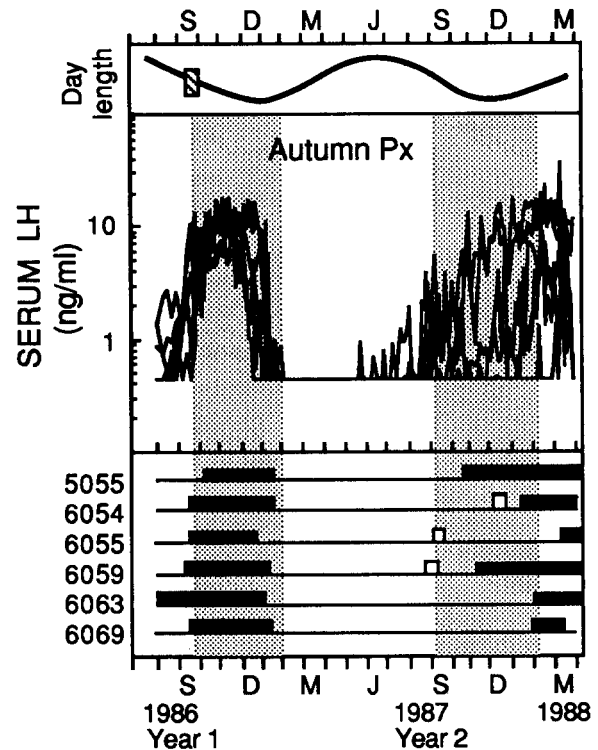


**Fig. 2.** Serum LH patterns in ewes pinealectomized around the summer solstice (Summer Px). Hatched bar in upper panel: time of pinealectomy. Middle and lower panels designed as in Fig. 1 (shaded area: mean period of elevated LH in the Control group for comparison). Open boxes in lower panel: periods of elevated LH that did not meet our criterion for a neuroendocrine breeding season (see Materials and methods)

Control group (Table 1). The duration of LH elevation was about half as long, and peak levels about half as great as those in the Control. In year 2 after pinealectomy, all ewes in this group showed LH rises that met the criteria for a neuroendocrine breeding season. The advanced onset of the LH rise seen in year 1 was maintained in 3 of the 6 ewes (#6012, 6014, 6018) in year 2. The onsets of these LH rises, however, were not synchronized among individuals (March 31 to September 11) and LH remained elevated well into the anestrus season of year 2 when observations were terminated (Fig. 2). Data were too variable to pool for group means in year 2.

#### *Autumnal-equinox pinealectomy (Fig. 3)*

All 6 ewes pinealectomized around the autumnal equinox showed an LH rise beginning in August–September. Onset time was not compared to that of the Control group because LH had risen in 3 ewes (#5055, 6059, 6069) prior to pinealectomy. Peak levels and duration of the LH elevation in year 1 were not different from those of the Control group, but the time of LH decline to baseline was 2.5 weeks earlier (Table 1). In year 2, all ewes showed LH rises that met the criteria for a neuroendocrine breeding season; however, the onset of



**Fig. 3.** Serum LH patterns in ewes pinealectomized around the autumnal equinox (Autumn Px). Figure designed as in Figs. 1 and 2

this rise was delayed and not synchronized among individuals (October 6–March 11) and was too variable to pool for data analysis.

#### *Winter-solstice pinealectomy (Fig. 4)*

Ewes pinealectomized around the winter solstice were approaching the end of the neuroendocrine breeding season at the time of surgery. The time of the LH decline to baseline, the duration of elevated LH, and peak LH levels were no different from those of the Control group. In year 2 of the study, however, there was a major alteration in the LH rise. In 3 of 6 ewes (#6042, 6056, 6065), the LH elevation began very late and it was still underway in two of them when the study was terminated in April. The remaining 3 ewes showed no discernable elevation in LH in year 2.

#### *Spring-equinox pinealectomy (Fig. 5)*

These ewes were pinealectomized in the early anestrus season and, because it was the last group, data are available for only one year after surgery. Onset of the LH rise subsequent to pinealectomy (year 2 of study) was markedly delayed compared with that of the Control group. The fall in LH back to baseline was also greatly affected in that LH had returned to baseline in only one of 6 ewes by the end of the study in April and,

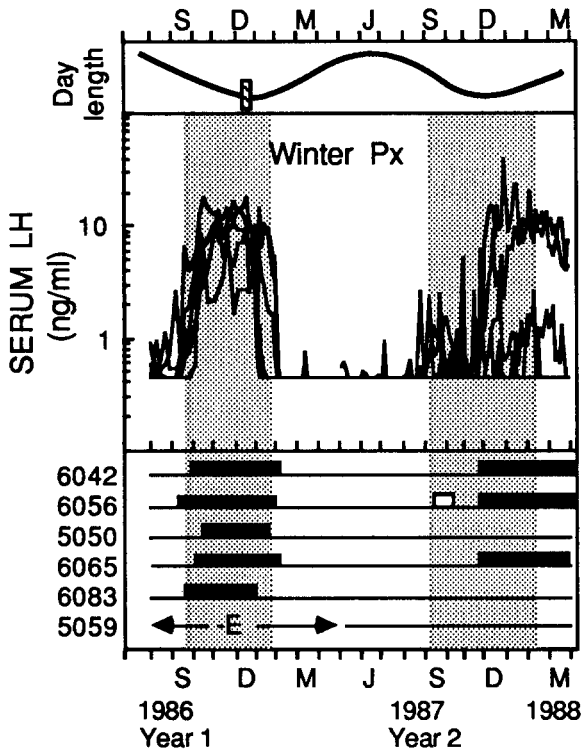


Fig. 4. Serum LH patterns in ewes pinealectomized around the winter solstice (Winter Px). Figure designed as in Figs. 1 and 2. '—E' with arrows in lower panel indicates period in which it was suspected that ewe # 5059 had an estradiol implant missing (LH values not included in top section of plot during this period)

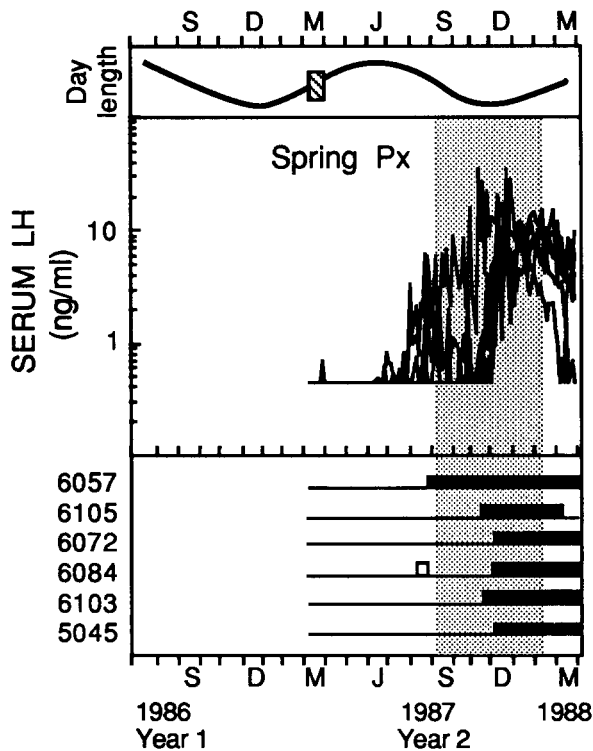


Fig. 5. Serum LH patterns in ewes pinealectomized around the spring equinox (Spring Px). Figure designed as in Figs. 1 and 2

in this ewe, the decline (March) was delayed relative to that of the Control group.

Infrequent observations of LH concentrations in all groups subsequent to this experiment indicate that LH eventually declined in all but one of the pinealectomized ewes that had elevated LH at the end of year 2 of the study.

**Discussion**

Our results support the hypothesis that different portions of the annual photoperiodic cycle play different roles in timing the breeding season of the ewe, an animal in which both seasonal reproductive transitions appear to be endogenously generated (Ducker et al. 1973; Worthy and Haresign 1983; Robinson and Karsch 1984; Robinson et al. 1985a; Worthy et al. 1985; Karsch et al. 1989). This is suggested by our finding that pinealectomy at various times of the year had different effects on both onset and duration of the subsequent breeding season. At some times (e.g., summer solstice), the effects of pinealectomy became evident within a month or two, whereas at other times (autumnal equinox) the response was not manifested until one year later. If we can accept that the response to pinealectomy is influenced by the animal's photoperiodic history and by that portion of the annual photoperiodic cycle which followed pinealectomy, we can begin to piece together the role played by different portions of the photoperiodic cycle in synchronizing the endogenous rhythm.

*Winter solstice to summer solstice*

Groups of ewes pinealectomized around the winter solstice and spring equinox showed delayed and variable LH rises during the breeding season of the following autumn. Specifically, in the Winter Px group, 3 of 6 ewes showed late onsets of the LH rise while the remaining animals did not show LH rises during the period of observation. Further, in the Spring Px group, 5 of the 6 ewes showed substantially delayed onsets of the LH rise. This suggests that lengthening days following the winter solstice synchronizes the breeding season to the appropriate time of year. It should be stressed that studies using other approaches support this conclusion. For example, by manipulating the photoperiodic environment of pineal-intact ewes, Malpaux and coworkers (1989) have found that the time of reproductive onset in the autumn depends upon the time of exposure to long days after the winter solstice. The more delayed the exposure to long days, the more delayed the onset of reproductive activity. Other studies have shown that another important role for long days is to break refractoriness to a short photoperiod, thereby restoring sensitivity to the decreasing day length which will occur after the summer solstice (Jackson et al. 1988).

The present findings might seem incongruous with the earlier report of Bittman et al. (1983a) that pinealectomy in late winter or mid-spring did not alter onset

of the breeding season the following autumn. This, however, is not necessarily inconsistent with our results, nor with the hypothesis that photoperiodic cues between the winter and summer solstices synchronize reproductive onset. Specifically, social cues from normal sheep can synchronize reproductive onset in ewes pinealectomized around the spring equinox (Wayne et al. 1989). The ewes pinealectomized by Bittman et al. (1983a) could have been synchronized by the intact ewes and rams with which they were maintained. Other findings that pinealectomy in mid-spring (April–May) disrupts onset of the breeding season of ewes isolated from intact sheep (Wayne 1988) supports this explanation and reinforces the view that the increasing day length of winter-spring provides a critical cue for timing the breeding season.

#### *Summer solstice to autumnal equinox*

During this quadrant of the year, the relatively long but decreasing day lengths appear to play 3 roles: 1) they suppress reproductive activity such that the breeding season does not begin until around the autumnal equinox; 2) they provide photoperiodic signals to maintain normal duration of the breeding season which is about to begin; 3) they provide a cue to attain maximal intensity of reproductive neuroendocrine induction during the upcoming breeding season. This is suggested by the finding that ewes pinealectomized around the summer solstice had an advanced LH rise that was low in amplitude and short in duration.

The conclusion that shortening days after the summer solstice increase the intensity of reproductive neuroendocrine induction is corroborated by studies using other experimental approaches. For example, the intensity of the reproductive neuroendocrine response in the pineal-intact ewe depends upon the strength of the inductive signal, i.e., by the 'shortness' of the short day (Robinson et al. 1985b; Robinson and Karsch 1987; Malpaux et al. 1988). In this regard, amplitude of the LH elevation was found to be greater in ewes transferred from a summer- to winter-solstice photoperiod (16L:8D to 10L:14D) than in those transferred from a summer-solstice to an autumnal-equinoctial photoperiod (16L:8D to 13L:11D) (Robinson and Karsch 1987). Our present observations, therefore, suggest that blocking the transduction of long-day cues around the summer solstice, by pinealectomy, provides a relatively weak inductive signal.

The hypothesis that decreasing day length provides a cue to maintain the breeding season is supported by studies in pineal-intact ewes using manipulations of artificial photoperiod to induce reproductive neuroendocrine activity (O'Callaghan et al. 1989a). Further, the progressive shortening of the day length itself appears important. In this regard, ewes experiencing a two-step photoperiodic decrease had a significantly longer period of reproductive activity than ewes experiencing only a one-step decrease to the same final day length (Malpaux et al. 1988; O'Callaghan et al. 1989b). Moreover,

transfer to a short photoperiod prolonged the neuroendocrine breeding season in ewes that had undergone a spontaneous increase in reproductive activity as a consequence of refractoriness to long days (Malpaux 1988). Not all studies, however, support such a maintenance role for decreasing photoperiod. For example, Jackson and coworkers (1988) observed that ewes moved indoors on the summer solstice, and kept on that photoperiod, had a breeding season no shorter than that of ewes kept outdoors. Other studies of similar design, however, have not confirmed that finding and, in fact, provide further evidence that the decreasing photoperiod after the summer solstice is needed to maintain the breeding season (Malpaux et al. 1989; O'Callaghan, Roche, Karsch, unpublished).

#### *Autumnal equinox to winter solstice*

Pinealectomy on the autumnal equinox had no major effect on any aspect of the neuroendocrine breeding season that was just beginning at the time of surgery. Only a small (2.5 week) advancement of the decline in LH was observed 4 months later, but this was too minor for a significant shortening of the LH elevation. It would appear, therefore, that once the breeding season has begun, essentially all relevant photoperiodic cues for that breeding season have been provided. This is not to imply, however, that the photoperiodic information perceived between the autumnal equinox and winter solstice is inconsequential for temporal organization of the seasonal reproductive cycle. In fact, this segment of the photoperiodic cycle likely plays an important role. Specifically, it serves to break long-day photorefractoriness (Jackson et al. 1988), thus ensuring the ewe can respond to the subsequent lengthening days that will synchronize the breeding season of the following year.

#### *Other interpretations and conclusions*

In keeping with the existence of an endogenous rhythm of reproduction that is entrained by photoperiod, our results could be interpreted in a somewhat different manner. Specifically, the winter-to-summer segment of the photoperiodic cycle could cause a phase advance of the reproductive rhythm because the breeding season was delayed when pinealectomy was performed on the winter solstice and the spring equinox. Conversely, the summer-to-autumn segment of the photoperiodic cycle could phase delay the rhythm because the onset and termination of the breeding season was advanced by pinealectomy on the summer solstice. Although our study was not designed to test this possibility, it is important to note that most of our ewes continued to exhibit rises and declines of LH into the second year after pinealectomy, with little or no apparent synchronization. The persistence of these changes in reproductive neuroendocrine condition can be accounted for by the endogenous circannual rhythm which was not synchronized by pho-

toperiod due to absence of the pineal. It is of interest in this regard that some studies suggest the neuroendocrine breeding season eventually becomes damped (Bittman et al. 1983a) or even disappears (Kennaway et al. 1984) with time after pinealectomy, although there is inconsistency in this point as other studies suggest the LH swings can persist for many years after surgery (Robinson and Karsch 1988).

At the outset of this discussion, it was stressed that our interpretations are based on the premise that the differential response to pinealectomy could be accounted for by photoperiodic history and the role played by that portion of the photoperiodic cycle which followed the surgery. There is, however, another factor which may also influence the response, namely the seasonal reproductive state at the time of surgery. In species which exhibit an endogenous circannual rhythm, the response to photoperiodic manipulation may vary according to stage of the rhythm, as is suggested by recent findings in the rainbow trout (Dustin and Bromage 1988) and possibly in the ewe (Jackson et al. 1989). It is important to note that, in our study, photoperiodic history could not be separated from stage of the annual reproductive cycle. It remains possible, therefore, that the differential responses to pinealectomy at different times of year could have depended upon the stage of the annual reproductive cycle rather than upon photoperiod.

In view of this possibility, it is pertinent to reiterate that studies using approaches other than pinealectomy have been performed to evaluate the importance of various portions of the photoperiodic cycle. In this regard, our interpretations of the response to pinealectomy are fully consistent with a recently developed model based on responses to photoperiodic manipulation of reproductive neuroendocrine activity in pineal-intact sheep (Malpaux et al. 1989). According to this model, an endogenous rhythm of reproduction drives the annual reproductive cycle. The primary role of photoperiod is to entrain this rhythm. The differing portions of the photoperiodic cycle appear to provide various types of regulatory cues (phase setting, duration of breeding season, inhibition/stimulation of the reproductive neuroendocrine axis, restoration of photosensitivity) each of which contributes to temporal regulation of the seasonal reproductive cycle of the ewe.

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