Review

Seasonality of reproduction in sheep

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Abstract

Unlike most domestic livestock species, sheep are widely known as an animal with marked seasonality of breeding activity. The annual cycle of daily photoperiod has been identified as the determinant factor of this phenomenon, while environmental temperature, nutritional status, social interactions, lambing date and lactation period are considered to modulate it. The aim of this paper is to review the current state of knowledge of the reproductive seasonality in sheep. Following general considerations concerning the importance of seasonal breeding as a reproductive strategy for the survival of species, the paper describes the manifestations of seasonality in both the ram and the ewe. Both determinant and modulating factors are developed and special emphasis is given to the neuroendocrine base of photoperiodic regulation of seasonal breeding. Other aspects such as the role of melatonin, the involvement of thyroid hormones and the concept of photorefractoriness are also reviewed.
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1. Introduction

Animals live under the influence of seasonal fluctuations of environmental conditions, with variable amplitudes frequently more marked in the higher latitudes and altitudes. The daily photoperiod and the annual cycles in environmental temperature are the most striking examples in temperate regions while the annual cycle in rainfall, with the consequent cycles in food availability, are important variables in tropical regions (Vivien-Roels and Pévet, 1983). As these changes reach acute levels, the animal species may respond by developing a series of different strategies (e.g. changing feeding habits, laying down energy reserves in the form of fat tissue, lowering the basal metabolism, moulting skin, fur and plumage, hibernating and migrating). Another mechanism is a reproductive strategy involving a 'natural contraceptive method' (Lincoln and Short, 1980) which restricts the reproductive activity to the best time of the year for assuring that births occur at a time that promotes maximal growth and development of the offspring and supports lactation in the mother (Wayne et al., 1989). In cold and temperate regions, this period corresponds to spring or early summer while in hot arid climates it coincides with the rainy season.

In order to synchronise their fertile period, seasonal breeders rely on environmental cues. Of the many environmental variables available, photoperiod is the most commonly used synchronising agent (Karsch et al., 1984) because unlike other climatic variables such as temperature and rainfall, the seasonal cycle of day length is constant between years. Species that use photoperiod to synchronise breeding activity

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are commonly classified in two different categories; long-day breeders or short-day breeders. Species in the first group, which include the ferret, the hedgehog and the horse, enter their breeding season after the winter solstice when the day length increases. Species in the second group, such as deer, goats and sheep, become sexually active in response to decreasing day length in the late summer to early autumn. It is important to stress that seasonal reproduction occurs mainly in wild species as a result of natural selection while animal domestication and artificial selection has contributed to minimise the effects of season on reproductive activity. This idea is supported by the study of Lincoln et al. (1990) who compared the reproductive seasonality of wild, feral and domesticated breeds of sheep kept under similar conditions at the same latitude and concluded that wild-type rams reached the peak of testicular activity later in the year than domesticated rams while the feral type followed an intermediate pattern. On the other hand, domestic species that breed throughout the year such as cattle and pigs, if left in the feral state for an extended period, gain a strong tendency for parturition to be seasonal (Ortavant et al., 1985).

It is clear from the literature that sheep breeds originating from temperate climates in mid or high latitudes are seasonal breeders and use the annual variation in daily photoperiod in timing the annual reproductive cycle. On the other hand, in tropical and sub-tropical environments ewes are either completely aseasonal or intermittently polyoestrus with the quality and availability of food dictating breeding activity. Supported by the works of Hafez (1952), Goot (1969) and Dyrmundsson (1978), Robinson (1981) argues that breeds whose origins are located between 35°N and 35°S have the tendency to breed at all times of the year while at latitudes greater than 35° it is normal to find ewes that are seasonally polyoestrus and whose breeding seasons are initiated by declining day length. In general, the higher the latitude the greater the photodependence and the more restricted the period of breeding activity (Poulton, 1987). In this view, while tropical breeds are sexually active throughout the year, British breeds demonstrate a distinct seasonality with a long anoestrous period during which no ewes ovulate spontaneously. Breeds from intermediate latitudes, such as the Australian Merino and Mediterranean breeds, have a short anoestrus dur-

ing which a proportion of ewes ovulate spontaneously (5% in Australian Merino; Martin et al., 1986). Within breeds there is also a large variation. As an example, some ewes of the breed Préalpes-du-Sud have a very short breeding season while others are almost aseasonal (Thimonier et al., 1986).

The breeding season starts in most ovine breeds during summer or early autumn (Chemineau et al., 1992) and its length varies largely among breeds but in general it ends during the winter (Hafez, 1952).

2. Manifestation of seasonality in the ewe

Reproductive seasonality in the ewe is characterised by changes at behavioural, endocrine and ovulatory levels, in an absolute fashion, giving rise to an annual alternation between two distinct periods; a breeding season, characterised by the succession at regular intervals (mean of 17 days) of oestrous behaviour and ovulation, if a pregnancy does not develop, and an anoestrous season characterised by the cessation of sexual activity. The transition from anoestrous to breeding season is gradual, with the occurrence of short cycles, because the first corpus luteum (CL) often regresses prematurely 5–6 days after its formation. Both ovulatory activity and oestrous behaviour show parallel seasonal variation but there are some discrepancies at the beginning and at the end of the sexual season when some ovulations are not accompanied by oestrus. It is only after the end of the first ovarian cycle that the behavioural oestrus is exhibited. Silent ovulations, not related either to the onset or the end of the sexual season, may also occur in some breeds during mid-anoestrus (Land et al., 1973; Ortavant et al., 1988). At the endocrine level, it is known that during the anoestrous season, follicle growth and regression occur and follicles as large as those found during the luteal phase of the oestrous cycle may be present (Hutchinson and Robertson, 1966; Matton et al., 1977; Webb and Gauld, 1985). Throughout seasonal anoestrus, the follicles produce steroids, and many of the positive and negative feedback effects of the steroids on secretion of luteinizing hormone (LH) continue as in the breeding season (Gordon, 1997). LH continues to be released, episodically, but with lower frequency than during the reproductive season (one pulse every 8–12 h against one pulse per 3–4 h

in the mid-luteal phase, one pulse per 1–2 h immediately prior to the preovulatory LH surge and one pulse every 20 min during the preovulatory LH surge (Yuthasastrakosol et al., 1977; Karsch, 1984; Martin, 1984; I'Anson and Legan, 1988; Thiéry and Martin, 1991). A major difference occurs also in plasma progesterone concentration which remains virtually at undetectable levels during anoestrus (Roche et al., 1970; Karsch, 1984; I'Anson and Legan, 1988). Follicle-stimulating hormone (FSH) levels seems not to be significantly different from those found during the reproductive season (Goding et al., 1969; Roche et al., 1970; Walton et al., 1977).

3. Manifestation of seasonality in the ram

Rams exhibit seasonal fluctuations in sexual behaviour, hormonal activity, gametogenesis and also in testicular weight and volume (Schanbacher and Lunstra, 1976; Lincoln and Davidson, 1977; Ortavant et al., 1985). However, behavioural and physiological variations are less pronounced than in the ewe. In fact, while ovulation and oestrus in the ewe is arrested, spermatogenesis and sexual activity in the ram never stop. Generally, all these parameters are high at the end of the summer and in autumn and low at the end of winter and in spring (Lincoln and Short, 1980; Haynes and Schanbacher, 1983; Pelletier and Almeida, 1987). Taking the Ile-de-France ram as an example and considering that similar tendencies have been observed in many other breeds, Ortavant et al. (1988) report that the testis weight can vary from 180–190 to 300–320 g and spermatozoa production per gram of testicular parenchyma can increase from 8.5×10^6 to 12.2×10^6, resulting in a daily sperm production variation per testis of 1×10^9 to 4.8×10^9. In Soay rams, LH and FSH levels begin to increase 2–4 weeks after the decrease in photoperiod, followed almost immediately by a rise in plasma testosterone levels accompanied by growth of the testis (Lincoln and Davidson, 1977). Rams' sensitivity to photoperiod is different from ewes. Sexual activity is usually stimulated 1–1.5 months earlier in rams, allowing that when the cyclic period of the ewes starts, the rams have already achieved a high level of sexual activity (this advancement is important because while anoestrous ewes can ovulate within a few days after hor-

monal stimulation due to the ever present large-sized follicles, the rams need approximately 45 days to complete spermatogenesis).

4. Modulating factors of seasonal breeding

It is well established that seasonal reproduction in sheep is mainly regulated by photoperiod. However, other cues from the environment (temperature, nutrition and social relationships) are believed to modulate its effect. While in temperate regions the photoperiod is the decisive factor and other environmental factors can only influence the onset and the duration of the anoestrous period, in tropical areas nutritional level is probably responsible for some seasonal acyclicity.

Environmental temperature cannot impose seasonality on reproductive activity of the ewe as was clearly demonstrated by Wodzicka-Tomaszewska et al. (1967). These authors found that in spite of dramatic changes in temperature, the annual rhythm of reproduction persisted in ewes kept under a constant photoperiodic schedule of 12 h of light–12 h of dark per day. However, temperature may modify the onset of sexual season. It has been shown that ewes maintained under low temperatures during the summer period began their reproductive season earlier than those kept under temperatures typical of that season (Dutt and Bush, 1955; Godley et al., 1966). Also, Lees (1966) found a positive correlation between mean temperature in July and the date of the onset of the breeding season in Clun ewes.

It is well known that nutrition affects many aspects of reproductive performance in sheep, e.g. age at puberty in both sexes, fertility, ovulation rate, embryo survival, parturition to re-breeding interval, testis growth and spermatozoa production (for details see Smith, 1991; Clarke and Tilbrook, 1992; Rhind, 1992; Robinson, 1996). Nutritional inadequacies can show their effects as short, middle and long-term. Thus, while some studies indicated that ewes can lose body weight without any immediate detrimental effect on reproductive performance, the accumulated losses over several reproductive cycles increase the incidence of barrenness (Robinson, 1981). The nutritional level received by ewes during the winter and spring can influence the percentage of ewes showing oestrus the following autumn (Smith, 1966) but a

sub-maintenance diet introduced before the onset did not delay the breeding season except in very young and very old ewes (Hafez, 1952). Forcada et al. (1992) found that the length of seasonal anoestrus was clearly reduced when Rasa Aragonesa ewes were maintained with low body condition score (2.5 as compared to 2.7) for two consecutive years. Thimonier et al. (1986) reported that the variations in the occurrence of births in regions where the rainfall is very variable can be explained by variations in food availability. In contrast, Gordon (1997) concluded that both in temperate and tropical breeds, the nutritional level appears to have little effect on the onset and duration of the breeding season. Robinson (1981) suggested that some conflicting reports in this matter can be resolved on the basis that reductions in body weight at mating of up to 15% have little detrimental effects in the short-term but reduce long-term production. In the ram, changes in nutrition lead to profound responses in testicular size and spermatogenic function (Martin and Walkden-Brown, 1995).

The mechanisms by which dietary nutrients regulate reproductive parameters are complex, not yet well understood and are the subject of speculation (Parr, 1987; Smith, 1991; Robinson, 1996). However, there are sound arguments to favour the hypotheses that feeding regimen affects the secretion or clearance of gonadotropins (effect on ovulation rate; Adams et al., 1997), the clearance of progesterone (effect on pregnancy rate; Parr, 1987) or the balance between FSH secretion and gonadal feedback by changing the responsiveness to the inhibitory effects of oestradiol and inhibin (effect on seasonality of reproduction; Boukhliq et al., 1996).

The reproductive season can also be influenced by lambing date. The onset and duration of the natural breeding season is affected by previous lambing date. An early lambing date is associated with an early onset of the subsequent breeding season (Haresign, 1992; Mitchell et al., 1997), but not with its cessation (Mitchell et al., 1997).

Lactation period is another factor that can affect the breeding season. Under normal conditions, in highly seasonal breeds, births occur during seasonal anoestrus and therefore in this situation lactational anoestrus cannot be identified. But when the ewes are induced to breed during seasonal anoestrus they lamb in the breeding season and in lactating animals the

resumption of ovarian activity is known to be delayed (Mallampati et al., 1971). Suckling has also a pronounced effect on the length of postpartum anoestrus in less seasonal breeds lambing naturally during the breeding season (Shevah et al., 1974; Pope et al., 1989). Denervation of the mammary gland has been proved to shorten the length of postpartum anoestrus (Kann and Martinet, 1975).

Social interactions can strongly affect the reproductive state of sheep. Relationships between and within sexes have been identified as influencing various parameters of reproduction in both the ewe and the ram. For details see the reviews of Thimonier et al. (2000) and Rosa and Bryant (2002).

5. The photoperiod as the determinant factor of seasonal reproduction in sheep

5.1. Experimental evidence

The role of day length as the deterministic factor in inducing and suppressing sexual activity in both the female and the male sheep has been clearly demonstrated in a variety of experiments. Artificial reversal of the annual rhythm of photoperiodic variations induces reversal of the period of ovulatory and oestrous activity in the ewe (Yates, 1949; Thwaites, 1965; Wodzicka-Tomaszewska et al., 1967) and of the periods of recrudescence and regression of testicular size (Alberio and Colas, 1976, reported by Ortavant et al., 1988) and sperm production in rams (Colas et al., 1985). The treatment of animals with a light regimen which mimics in 6 months the normal annual day length pattern, generate in the ewe two reproductive seasons (Ortavant and Thibault, 1956, reported by Pelletier and Almeida, 1987) and in the rams two cycles of testicular growth (Lindsay et al., 1984) and sperm production (Jackson and Williams, 1973) in 1 year. Finally, the alternation of 3- or 4-month periods of constant long (16 h of light–8 h of dark) and constant short (8 h of light–16 h of dark) days induces the alternation of periods of sexual activity and inactivity in the ewe (Legan and Karsch, 1980) and testicular growth in the ram (Lincoln and Davidson, 1977). If the periods of day length are alternated every month, rams show a progressive increase in testicular weight which finally remains steady close to the maximum

level (Pelletier and Almeida, 1987). Different light protocol treatments which produced changes in reproductive activity in both sexes can also be seen in the review of Chemineau et al. (1992).

5.2. Neuroendocrine mechanisms involved in the photoperiodic control of reproduction

The answer to the intriguing question of what causes ovulation to cease during seasonal anoestrus requires a full understanding of the hormonal patterns and mechanisms involved in the governing of ovarian activity during not only the period of anoestrus but also the periods of transition to anoestrus and return to oestrus. The present section will focus on these points and conclude with the presentation of the current model of the neuroendocrine regulation of seasonal anoestrus.

5.2.1. Hormonal pattern during the transition to seasonal anoestrus

One of the first attempts to characterise the hormonal changes during the period of transition from cyclicity to seasonal anoestrus in ewes was made by Rawlings et al. (1977). These authors did not detect any gradual changes in the concentrations of LH, oestradiol and progesterone, but noted that at the end of the last cycle some ewes experienced a subnormal rise in LH concentration after which both LH and oestradiol levels remained basal. In more elaborate studies Karsch et al. (1980) and Legan et al. (1981) found that the pattern of LH secretion following the regression of the last CL of the reproductive season is different from those of previous luteolyses. While during the breeding season the basal LH level increases in a sustained way for 48 h, during transition to anoestrus it starts to increase for the first 24 h but falls progressively in the next 24 h. In addition, there is no occurrence of oestradiol rise and LH surge.

5.2.2. Hormonal pattern during seasonal anoestrus

A brief description of the hormonal relationships during the non-breeding season and some bibliographic support has already been presented in Section 2. Throughout this period the levels of progesterone remain low and no gonadotrophins surges are observed. However, neither the ovary nor the LH pulse generating system are inactive. Follicular

development does not stop, periods of early follicle growth and regression are taking place and mature follicles are present. The study of follicular dynamics by ultrasonography has shown the existence of waves of follicular development (Souza et al., 1997). The follicles produce steroids, and are capable of ovulating. Gonadotrophin hormones are secreted and both positive and negative feedback effects of ovarian steroids on gonadotrophin secretion are readily demonstrable (Legan and Karsch, 1979). Oestradiol secretion is similar to the breeding season, that is an oestradiol rise follows each LH pulse (Scaramuzzi and Baird, 1977). In fact, the follicles are responsive to gonadotrophin stimulation and ovulation can occur if anoestrous ewes are treated with exogenous gonadotrophin-releasing hormone (GnRH) (Haresign et al., 1975; Southee et al., 1988) or multiple injections of LH (McNeilly et al., 1982). However, the LH pulse generating system, although active, is compromised because both frequencies of GnRH (Barrell et al., 1992) and LH (Karsch, 1984) are extremely low, tending to be even less than during the luteal phase of the cycle and sustained increases in tonic LH secretion are not normally observed (Scaramuzzi and Baird, 1977). Barrell et al. (1992) found that in marked contrast with observations made during the breeding season, an increased pulse frequency of both GnRH and LH hormones is not observed in anoestrus, which leads to the conclusion that the switch from breeding to anoestrous season in the ewe is associated with a marked change in the GnRH neurosecretory system.

5.2.3. Hormonal pattern during the transition from anoestrous to the breeding season

Yuthasastrakosol et al. (1973) first reported data suggesting the occurrence of minor LH surges during late anoestrus and the existence of a rise in progesterone levels commencing 11–15 days before the first behavioural oestrus. In a more elaborate work, Yuthasastrakosol et al. (1975) determined the levels of oestrogen, progesterone and LH throughout anoestrus and the first oestrous cycle of the breeding season. Once again, exceptionally high levels of LH were observed in late anoestrus, more precisely on day 24 before oestrus and minor rises of progesterone also occurred around this period. I'Anson and Legan (1988), using a more frequent blood sampling regime, also confirmed the occurrence of these brief increments in

LH and progesterone levels before the first full-length luteal phase of the breeding season. In this study, 75% of the observed increases in LH pulse frequency occurred within 1 week after a low frequency pattern of secretion (full anoestrus) and within 1 week before a rise in progesterone. These results suggested that the breeding season commences with an increase in tonic LH secretion which initiates the sequence of preovulatory events leading to the first LH surge and that these changes in LH secretion pattern occur rapidly within less than a week. According to the authors, the transient increments in progesterone may represent short luteal phases which result from ovulation of immature follicles. Finally, I'Anson and Legan (1988) suggested that before the first oestrous cycle, a transition period of 1–4 weeks exists, during which one or more increases in LH pulse frequency and progesterone concentrations may occur.

5.2.4. Current model of the photoperiodic control of reproduction

It seems clear that the start of seasonal anoestrous condition in the ewe results from the interruption of the preovulatory sequence of events leading up to ovulation. In order to detect in which step the sequence is interrupted, Legan and Karsch (1979) studied all the progression of events, beginning with the LH surge and working back. Following various considerations, they suggested that the primary cause of seasonal anoestrus is not failure of the LH surge, behavioural oestrus or absence of oestradiol rise or any mechanism associated with these events. These considerations have later received much support and it is now well known that all preovulatory events and ovulation can be induced in seasonally anovular ewes if they are treated with multiple injections of GnRH (McLeod et al., 1982; Southee et al., 1988). This leaves only the first step in the sequence of events leading up to ovulation—the sustained increase in basal LH secretion (or GnRH, as this hormone dictates the secretion of LH). A necessary condition for this hypothesis to be correct (i.e. the disruption of a sustained increase in basal LH secretion to be the responsible for the establishment of seasonal anoestrous) is that a sustained 48 h increase in tonic LH secretion should not be observed in three situations: firstly, following the brief episodes of elevated LH levels during anoestrus, secondly, following a treatment of progesterone in the anoestrous season and thirdly, following the regression of the last CL of the breeding season. All these premises have been confirmed as reported above in this section. The question that naturally arises at this point is what prevents the sustained preovulatory increase in LH secretion during anoestrus.

The clue to answer this question was first provided by the observation that during the breeding season, each preovulatory rise of oestradiol was accompanied by a sustained parallel increase in LH while in anoestrus an induced oestradiol rise was accompanied by a pronounced drop in LH levels (Legan and Karsch, 1979). These opposite actions of oestradiol would suggest that in the anoestrous season this steroid exerts a strong negative feedback effect on LH secretion. Probably the first convincing evidence that there is a seasonal shift in the ability of oestradiol to inhibit LH secretion was provided by the work of Legan et al. (1977). In their study, in which a group of ovariectomised ewes were treated with oestradiol implants, a marked seasonal change in circulating LH was observed. During the breeding season, LH was elevated but in anoestrus the level of this hormone was undetectable. On the contrary, in the control group (ovariectomised ewes without implants) no major seasonal variation was detected, with the LH concentration being elevated and maintained at levels similar to those of the reproductive season in oestradiol treated ewes. This study also showed a coincidence between the periods of changes in LH response to oestradiol (2–3 weeks) and the periods of transition between breeding and anoestrous seasons in intact ewes.

The considerations presented above, together with the proven fact that the response of LH secretion to oestradiol is controlled by photoperiod (Legan and Karsch, 1980), led Karsch et al. (1980) to formulate an hypothesis for the photoneuroendocrine control of seasonal breeding in the ewe. According to this hypothesis, during the breeding season the responsiveness of the neuroendocrine system to the oestradiol negative feedback is low and consequently, following the regression of each CL, all the preovulatory events can occur. During transition to anoestrus, the response to oestradiol inhibition of LH starts increasing and when the last CL of the breeding season regresses, tonic LH secretion begins to increase but this increase is not sustained because the accompanying onset of oestradiol rise prevents it. In the absence of a suitable stimulus,

oestradiol would not reach the threshold necessary to switch to positive feedback over LH, and as a consequence LH surge and ovulation does not occur. At the end of anoestrus, as the responsiveness to oestradiol negative feedback diminishes, the sustained increases in LH and oestradiol become possible again, thus enabling oestradiol to reach the threshold for eliciting the preovulatory LH surge allowing oestrous cyclicity to be re-established.

The described hypothetical model for the control of seasonal breeding in the ewe only took into account the seasonal change in the ability of the LH pulse generating system to become more or less sensitive to the negative feedback effect of oestradiol, indicating a photoperiodic-induced variation of this mechanism. There is, however, evidence that photoperiod also has a direct effect on the LH pulse generator, independently of the action of steroids. This effect has been observed in castrated rams kept under controlled photoperiod (Pelletier and Ortavant, 1975) and in long-term ovariectomised, not oestradiol treated ewes, exposed to the annual cycle of natural photoperiod (Goodman et al., 1982; Robinson et al., 1985a; Thomas et al., 1988) or submitted to artificial controlled photoperiods (Robinson, 1983). In all cases, LH pulse frequency increased as days became shorter and declined as day length increased.

Although the relationship between these two effects and its importance remains to be established, the overall perception collected from the literature is that quantitatively the oestradiol feedback mechanism seems to account for much of the reduction in LH pulse frequency. Giving more support for this view, Karsch et al. (1993) were unable to find a significant seasonal difference in the frequency of both GnRH and LH pulsatility in ovariectomised ewes not treated with oestradiol (although trends for a reduced rate in anoestrus were apparent) while oestradiol implants produced a profound suppression of the frequency of these hormones. Similar results for GnRH secretion were obtained by Karsch et al. (1987).

The current model for photoperiodic control of ovarian cyclicity was enunciated by Karsch et al. (1984) and is very much based on the described model proposed by Karsch et al. (1980) but in which the effect of the direct photoperiod drive was incorporated. In short, it suggests that under the inductive influence of short days of the breeding season, there is a high drive

to the LH pulse generator eliciting high frequency of GnRH discharges from the hypothalamus and in addition, under such photoperiod, the negative feedback effect of oestradiol is not strong enough to suppress LH release. Therefore, the frequency of LH pulses can increase sufficiently for the accomplishment of the preovulatory sequence and ovulation occurs. Under the inhibitory influence of long days in the anoestrous season there is a low drive to the LH pulse generator and additionally the pulse generator becomes very sensitive to the negative feedback action of oestradiol. Consequently, the low pulsatility of LH does not provide sufficient stimulation to support a sustained oestradiol increase and the preovulatory sequence cannot take place as a result the oestrous cyclicity is arrested.

It is now well established that the negative feedback action of oestradiol on LH secretion is brought about via a reduction in the GnRH pulse secretion rather than a major diminution of pituitary responsiveness to GnRH (Karsch et al., 1987, 1993; Barrell et al., 1992). The mechanisms by which changes in environmental photoperiod induce different responses of the GnRH neurosecretory system to the same pattern of oestradiol secretion remains to be elucidated. An important point to stress is that the GnRH neurones in sheep (Lehman and Karsch, 1993; Herbison et al., 1993; Herbison, 1995), as well as in other mammals (Shivers et al., 1983; Herbison, 1995), do not seem to have steroid receptors which add more complexity to this matter. However, it is known that there are many afferents to GnRH neurones which have the potential to receive and transmit steroidal feedback signals (Tilbrook and Clarke, 2001). In this regard, it has been suggested that the response to oestradiol negative feedback that leads to anoestrus involve afferents from other neurones (Xiong et al., 1997; Lehman et al., 1997). This fact could lead to the speculation that seasonality is not due to changes in GnRH neurones but rather to changes in afferent neurones which regulate GnRH neurosecretion. However, this is probably not entirely the case, and some action may be reserved to the GnRH neurones, since the study of Xiong et al. (1997) has shown evidence that seasonality may induce morphological changes in GnRH cell bodies.

As the most seasonal hormonal variation occurs in prolactin concentration, with highest levels coinciding with long days and lowest levels coinciding with

short days (Kennaway et al., 1987), and since high prolactin levels are normally associated with ovarian inactivity, it has been suggested that the seasonally high prolactin concentration may be responsible for the seasonal impairment of reproductive function in the sheep (Walton et al., 1977, 1980). However there is little evidence for such a role of prolactin. Experiments carried out both in the ram and in the ewe in which manipulation of photoperiod have been used to dissociate the pattern of prolactin secretion from seasonal reproductive changes have shown that regression of the testes still occur when rams have low levels of prolactin (Almeida and Lincoln, 1984), and ewes show oestrous cyclicity at times when prolactin concentrations are high (Worthy et al., 1985; Jackson and Jansen, 1991). Detailed information about the seasonal prolactin secretion and its role in seasonal reproduction in sheep and other mammals is provided by the review of Curlewis (1992).

5.3. Transfer of photoperiodic information to the hypothalamo–pituitary axis

From the discussion presented in the previous section, it is clear that the seasonality of reproductive activity in sheep is primarily due to changes in the responsiveness of the GnRH neurosecretory system to the negative feedback action of oestradiol, which in turn are dictated by variations in length of the daily photoperiod. The next sections are intended to review the way by which photic information from the environment is received, transmitted and measured throughout the neuroendocrine system and the role played by photoperiod in timing the beginning and the end of the breeding season.

5.3.1. Anatomical pathway

The photoneuroendocrine pathway whereby photic cues are picked up and relayed to the GnRH generating system has been extensively investigated and is now well understood (Legan and Winans, 1981; Karsch, 1984; Karsch et al., 1984; Turek et al., 1984; Hansen, 1985; Lincoln, 1992). Based on evidence obtained mostly in hamsters, Legan and Winans (1981) first proposed the current model for the pathway in sheep which since then has received much additional experimental support. According to this model, the photic stimuli are first received by the retina which contains the photoreceptors necessary for the photoperiodic control of reproduction in this species. The photic information is then transmitted from these receptors to the suprachiasmatic nuclei (SCN) of the hypothalamus via a monosynaptic tract known as the retinohypothalamic tract. The SCN functions as an internal biological clock regulating endogenous circadian rhythms. After receiving input from the circadian system, the photoperiodic message is transmitted to the pineal gland by way of its sympathetic innervation designated by superior cervical ganglia (SCG). The pineal gland functions as a transducer converting neural information regarding the light-dark cycle into a hormonal signal which take the form of a circadian rhythm of melatonin secretion. The pattern of this melatonin signal, which can be interpreted as inductive or suppressive, sets the frequency of the LH pulse generating system and determines its capacity to respond to the negative feedback action of oestradiol (Lincoln, 1992; Williams and Helliwell, 1993; Malpaux et al., 1996).

Experimental evidence for the existence and functioning of the described retinohypothalamic tract has been provided by various studies, based mainly in the destruction of its components, which have shown that the interruption of this pathway renders the animals unresponsive to changes in day length and interferes with the secretion of melatonin. Legan and Karsch (1983) and Karsch et al. (1984) found that the photoperiodic control was lost in ewes following blinding, demonstrating the role of the photoreceptors located in the eyes. A monosynaptic tract, independent of the primary optic tract used for visual image perception, linking the retina to the SCN, previously identified in other species, has also been found in sheep by Legan and Winans (1981) using a technique involving the autoradiographic localisation of [3H] proline. The implication of the SCN has been shown by Przekop and Domanski (1980), Jackson et al. (1986) and more recently by Scott et al. (1995) after confirmation that the ewes would not respond to day length changes following the lesion of this section of the brain. Both the removal of the superior cervical ganglionectomy (SCG) or the pineal gland resulted in an inability of rams (Lincoln, 1979; Lincoln et al., 1989) and ewes (Bittman and Karsch, 1984) to respond to changes in photoperiod, confirming the indispensability of those anatomic structures.

5.3.2. The role of melatonin

Melatonin is the main hormone secreted by the pineal gland and is by far the most extensively studied pineal compound. In several species, melatonin can also be synthesised in other organs such as the retina, intestine and salivary glands (Vivien-Roels and Pévet, 1983) but in most mammals the pineal gland accounts for almost all the melatonin in circulation (Yellon et al., 1992). Numerous studies have provided evidence that the pattern of secretion of this hormone follows a circadian rhythm with significant secretion occurring only during the dark period of the day with the light acting as a supressor. Consequently, melatonin levels in both the pineal gland and the blood are high at night and low during the day. There is also experimental evidence to show that exposure of animals to light at night readily suppresses the secretion of melatonin (Lincoln, 1992). The question of which parameter of the nightly melatonin secretion is used to measure the day length (i. e. amplitude, duration or phase relative to the 24 h light/dark period) has been extensively discussed in the literature. From the two major hypotheses that have emerged, the "phase hypothesis" and the "duration hypothesis", it seems that the most convincing evidence to date supports the "duration hypothesis" because sheep have been shown to respond to the melatonin signal irrespective of when it is received during the 24 h period (Wayne et al., 1988). Therefore, the duration of nocturnal elevation in melatonin level may constitute the message whereby the pineal mediates the photoperiodic regulation of hormonal secretion. Long days are characterised by a short duration of melatonin secretion while short days are characterised by a longer duration of secretion. However, the circadian rhythm persists in constant darkness, being eliminated in constant light (Rollag and Niswender, 1976) or when animals are submitted to pinealectomy or superior cervical ganglionectomy when melatonin is secreted in small or undetectable amounts (see Deveson et al., 1992 for review). This indicates that the rhythm is generated endogenously, presumably under the control of the SCN. The definitive demonstration that melatonin influences the reproductive seasonality in sheep came from studies in which melatonin was infused into pinealectomised ewes in patterns mimicking long and short days and it was found that the reproductive response was similar to pineal-intact ewes experiencing those photoperiods (Bittman and Karsch, 1984; Karsch et al., 1984; Bittman et al., 1985).

The major question being addressed at this stage of the discussion relates to the way by which the melatonin secretion pattern operates to change the sensitivity of the GnRH pulse generator to the oestradiol negative feedback. The sites and mechanisms of action of melatonin have been extensively studied and reviewed in the literature (Kennaway and Hugel, 1992; Williams and Helliwell, 1993; Kennaway and Rowe, 1995; Malpaux et al., 1996; Goldman, 2001) and yet there is still no clear indication of where and how melatonin acts. Although melatonin may act at different levels of the reproductive system, the main action may be within the central nervous system. Indeed, a direct effect of melatonin on GnRH secretion was demonstrated by Viguié et al. (1995) who observed an increase in GnRH pulse frequency when ovariectomised oestradiol treated ewes exposed to long days received melatonin implants. The rise in GnRH pulse frequency occurred simultaneously with an increase in LH pulsatility 40–60 days after the beginning of melatonin treatment. However, according to Malpaux et al. (1996), a direct action of melatonin on GnRH neurones appears unlikely. One reason is because most of the GnRH neurones are located in the preoptic area (POA) of the hypothalamus which does not seem to be a site of action of melatonin and very few are located in the mediobasal hypothalamus (MBH) which is a putative site of action of this hormone. Also, the long delay in the GnRH and LH responses to the melatonin treatment suggests a more complex mechanism and several neurotransmitters have already been implicated in the process, such as dopamine, serotonin and excitatory amino acids (glutamate, aspartate, etc.) (Malpaux et al., 1996). The detection of the physiological sites of action of melatonin has been attempted using melatonin microimplants inserted into regions of the hypothalamo–hypophisial complex which limits the delivery of this hormone to those sites, in animals maintained in a photoperiod of long days. Results from this sort of study have shown that microimplants positioned in the premammilary hypothalamic area (PMH) (Malpaux et al., 1998) and in the MBH but not in the POA induced an increase in LH secretion in ewes (Malpaux et al., 1993) and an increase in FSH secretion and testicular size in rams (Lincoln and Maeda, 1992). On the other hand, several studies have

shown that the sheep pars tuberalis (PT) is also an important site of melatonin action (De Reviers et al., 1989; Morgan et al., 1989; Bittman and Weaver, 1990; Stankov et al., 1991) but it is not clear whether this is a crucial target for reproductive action. In fact, while Lincoln (1994) reported that the administration of melatonin in the PT affected the photoperiodically induced cycles of FSH and prolactin secretion in rams, other authors (Malpaux et al., 1994, 1995, 1998; Goldman, 2001) argue that melatonin in this site only regulates the seasonal variation in prolactin secretion and not the secretion of gonadotropins. But whatever the mechanism and site of action of melatonin, its administration either by daily dosing or through constant-release devices allows short days to be mimicked and therefore it can be used to control the seasonal reproduction in both the ram and the ewe. However, for the treatment to be effective the animals have to have pre-experienced a period of exposure to long days just before receiving the melatonin and the response takes 2–3 weeks in the ram (Chemineau et al., 1992) and 40–60 days in the ewe (Haresign, 1992; Viguié et al., 1995) to be achieved.

Considering the fact that there are breed differences in the reproductive response of sheep to changes in photoperiod and that seasonal reproduction is driven by the pattern of melatonin secretion, it could be expected that breed differences would be due to different genetic abilities to secrete melatonin. However this does not seem to be the case since Lincoln et al. (1990) report examples in which the same pattern of melatonin secretion (i.e. the duration of the period of elevated levels reflects the period of darkness) is found among breeds which differ in the degree of seasonality of reproduction. Therefore, it may not be the melatonin signal which differs between breeds but the way the signal is translated in the brain.

5.4. Regulation of the annual reproductive cycle

First of all, it is important to stress the existence in the sheep of an endogenous circannual rhythm of reproductive neuroendocrine function which means that seasonality persists in the absence of photoperiodic information. Evidence for such endogenous rhythmicity is provided by the fact that long term changes in reproductive condition continue to be expressed during prolonged exposure of animals to a constant day length

(Howles et al., 1982; Karsch et al., 1989; Jackson and Kao, 1990), or following procedures that functionally block the transmission of photoperiodic information to the GnRH pulse generating system such as surgical blinding (Legan and Karsch, 1983), pinealectomy (Barrell and Lapwood, 1979; Kennaway et al., 1984; Lincoln et al., 1989) or superior cervical ganglionectomy (Lincoln et al., 1989). However, the reproductive shifts are neither synchronised among animals nor in phase with the natural breeding cycle. In this context, the prevailing current view is that the seasonal reproduction in sheep is generated by an endogenous circannual rhythm of reproductive neuroendocrine activity and that the role of photoperiod is to synchronise but not to create this rhythm (Karsch et al., 1989; Malpaux et al., 1989; Woodfill et al., 1994; Barrell et al., 2000). The mechanism by which photoperiod synchronises the rhythm is not yet well understood. However, it seems that not all photoperiodic information of the year is required for animals to synchronise the rhythm and that not all portions of the annual photoperiodic cycle are equally effective at synchronising it. Woodfill et al. (1991) found that pinealectomised ewes exhibited synchronous annual reproductive cycles when treated with only a 70-day block of a long-day pattern of melatonin each 365 days. Malpaux et al. (1989) reported findings which led them to conclude that it is the time at which increasing photoperiod is first experienced in late winter or spring that determines when the subsequent breeding season begins. In one of their experiments in which ewes were exposed to increases in day length at different time-intervals after the winter solstice, these workers found that when ewes perceived long days earlier than normal, the breeding season was advanced. In contrast, when ewes perceived long days later, the breeding season was delayed. These authors concluded that long days play a critical role in positioning the breeding season to the autumn. All these results were confirmed by the study of Woodfill et al. (1994) who found that the annual rhythm can effectively be synchronised with a period of 90 days of long-day photoperiodic cues (summer melatonin pattern) perceived around the summer solstice. During winter, the melatonin pattern secreted at that time fails to synchronise the rhythm. Recently, the work of Barrell et al. (2000) demonstrated the inability of the winter melatonin pattern to entrain the rhythm also during the summer

stage of the rhythm. These findings indicate that the mere presence of a circadian melatonin pattern is insufficient for rhythm entertainment. What really determines entrainment seems to be the characteristics of the pattern, particularly the pattern that mimics the photoperiodic signals of summer. Adding to this, the findings that the summer pattern applied during winter (Woodfill et al., 1991) or at random stages of the free-running rhythm (Woodfill et al., 1992) synchronises the rhythm, finally allows the inference that the synchronisation of the circannual reproductive rhythm of sheep is dependent on the quality of the photoperiodic signal (i.e. the summer photoperiodic signal) and not on the rhythm stage.

5.5. Photorefractoriness

Under natural conditions, sheep breed during the autumn when the increasing duration of the melatonin signal appears to be stimulatory to reproductive activity. However, ewes maintained on stimulatory short days eventually cease breeding activity (Robinson and Karsch, 1984; Minton, 1990). Conversely, ewes kept on long day lengths which are considered to be inhibitory to reproduction become reproductively active after some time (Worthy et al., 1985; Robinson et al., 1985b). The rams also perform in a similar way and if left in the natural annual photoperiodic cycle, the LH and testosterone blood levels as well as the testicular weight start increasing generally before the summer solstice (Pelletier and Almeida, 1987) when day length is still increasing and therefore not stimulating for reproductive activity. On the other hand, in natural conditions, the same photoperiod occurs twice a year in a symmetric fashion in relation to the solstices. However, sheep are reproductively stimulated at one time of the year but inhibited under the same photoperiod at the other. The preceding considerations provide evidence that the timing of onset and cessation of the reproductive season is not regulated by an absolute critical day length, rather it is highly dictated by the recent photoperiodic history experienced by the animal. The assumption of this phenomenon led to the emergence of the concept of photorefractoriness. According to this concept, if an animal is exposed to a fixed photoperiod for a prolonged period (in sheep, 30–32 weeks for gradual shifts under natural conditions or 16–18 weeks for artificial abrupt

shifts, Nicholls et al., 1989) it loses the reproductive response to that photoperiod and it is said to be photorefractory (Robinson and Karsch, 1987; Williams and Helliwell, 1993). Sheep can be refractory to either long or short days. In this view, and according to Malpaux et al. (1989) and Minton (1990) the onset of anoestrous in ewes in late winter/early spring is not brought on by the arrival of long days; rather the ewes cease reproductive activity because they become insensitive to stimulatory short days. Similarly, ewes start ovulating in late summer/early autumn not because of the exposure to short days but because they are no longer inhibited by long days. Since the transition from anoestrus to breeding season does not require a decrease in day length and because reductions in photoperiod prolong the period of reproductive activity (Malpaux et al., 1988a, 1989; Nicholls et al., 1989; Malpaux and Karsch, 1990) it has been suggested that in natural conditions the role of long days is to synchronise the onset of the breeding season while short days play the determining role in sustaining it (Malpaux et al., 1989; Malpaux and Karsch, 1990).

It has been shown that the lack of response to a fixed photoperiod is not due to a change in the circadian pattern of melatonin secretion (Karsch et al., 1986; Malpaux et al., 1987, 1988b) and therefore it may be caused by a change in the response of the endocrine system to the melatonin signal as was first suggested in the case of hamsters by Bittman (1978) and later in sheep by Karsch et al. (1986).

5.6. The role of thyroid hormones in seasonal reproduction

Thyroid hormones play an important role for reproductive seasonality in a large range of species including birds, rodents and mammals. The first evidence of the involvement of these hormones in seasonal reproduction of sheep was provided by Nicholls et al. (1989) who found that ewes thyroidectomised in late anoestrous season entered normally into the breeding season but continued to exhibit regular oestrous cycles throughout the following anoestrous season, remaining in this condition for more than 1 year. It is now well known that thyroid hormones do not influence transition into the breeding season but their presence is required for its termination. Therefore, in the absence of these hormones the seasonal reproductive rhythm

is not expressed. The site and mechanism of action of thyroid hormones remain to be elucidated but according to Karsch et al. (1995) it may act within the brain to promote morphological changes in the GnRH neurosecretory system. Therefore, the way in which the thyroidectomy prevents the effect of season on reproduction does not appear to be due to an altered metabolism of steroid hormones, to a disruption of all seasonal processes or to a disturbance of the pathway responsible for the transduction of the photoperiodic stimuli. Rather, the effect of thyroidectomy seems to be more specific, being restricted to the seasonal increase of the oestradiol negative feedback on GnRH release (Dahl et al., 1994, 1995). More detailed information on the involvement of thyroid hormones in seasonal reproduction is provided by the reviews of Karsch et al. (1995) and Gerlach and Aurich (2000).

The seasonal reproduction and the endocrine mechanisms involved can largely be influenced by behavioural stimuli released through the social relationships that an animal (both the ram and the ewe) establishes with others of the same species. This important aspect of the reproductive process in sheep was recently reviewed by Rosa and Bryant (2002).

6. Conclusion

Seasonality of the reproductive activity in sheep is a general phenomenon for mid and high-latitude breeds. The seasonal variations in mating concern both males and females. However, variations in gonadal activity and sexual behaviour are less pronounced in the ram than in the ewe. While in rams spermatogenesis and sexual activity never stop, in ewes ovulation and oestrus is arrested during variable periods. The daily photoperiod has long been identified as the determinant factor of seasonal breeding while environmental temperature, nutrition, behaviour, lambing date and lactation period exerts a modulator effect. The central aspect of the current model of the photoperiodic control of seasonality is that under the influence of long days in the anoestrous season the LH pulse generating system becomes very sensitive to the negative feedback action of steroids. The mechanisms involved are complex and not entirely understood. Melatonin, through its duration of nocturnal secretion, is the hormone responsible for the translation of the day length

information to the reproductive axis by changing the sensitivity of the GnRH pulse generator with consequent modification on the pulsatile secretion of LH. The exact site of action of melatonin within the central nervous system is still controversial and requires further research. Studies using melatonin microimplants have indicated that the premammilary and the mediobasal but not the preoptic areas of the hypothalamus are physiological sites of action of melatonin involved in the control of seasonal reproduction. The pars tuberalis, even though having been recognised as an important site of melatonin action, is not consensually considered as being a crucial target for reproductive action.

Photoperiod is responsible for the synchronisation of reproductive activity with the environment but not for the generation of a circannual reproductive rhythm. In fact an endogenous rhythm exists in the absence of any photic stimulus and therefore the role of photoperiod is to synchronise but not to create this rhythm. It has recently been demonstrated that not all photoperiodic information of the year is required for animals to synchronise the rhythm and that not all portions of the annual photoperiodic cycle are effective at synchronising it. The winter pattern of melatonin secretion fails to synchronise the rhythm at any time of the year. On the other hand the summer melatonin pattern is effective at synchronising during the summer and indications are that it is also effective in any other period of the year. However this subject requires further investigation.

Finally, it should be considered that the thyroid hormones also have an important role in seasonal reproduction but the site, the mechanisms of action and its integration in the current neuroendocrine model of photoperiodic control of seasonal reproduction need to be elucidated.

Acknowledgements

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