

A critique of the evidence on the importance of steroid feedback to seasonal changes in gonadotrophin secretion

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Introduction

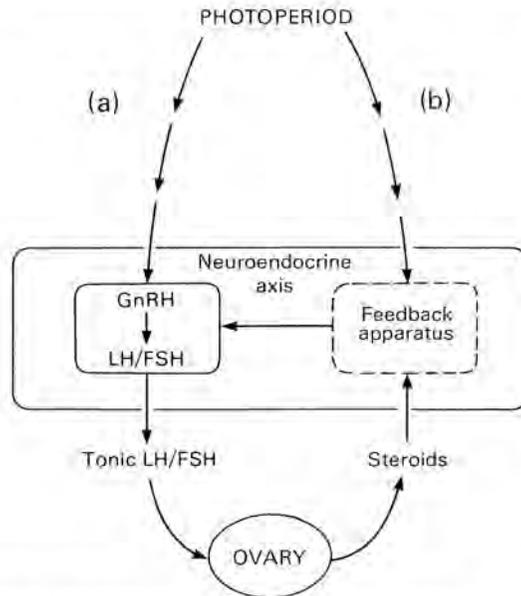
Casual observation of farm animals immediately points to some basic differences in their reproductive function; namely, some species (sheep and horses) have distinct breeding seasons while others (cows and pigs) do not. The seasonal nature of reproduction in the former is not only of immense practical importance to the agricultural industry but is also of considerable theoretical interest to the reproductive endocrinologist. The demonstration that photoperiod is the primary environmental cue controlling reproduction in sheep (Yeates, 1949; Hafez, 1952) raises several intriguing questions including: How does the sheep measure the length of the day? How is photoperiodic information transferred from the photoreceptor to the hypothalamo-hypophysial axis? What changes in the hypothalamo-hypophysial axis determine the reproductive capacity of the gonads? In this paper we will concentrate on the last question.

In both the ram (Pelletier & Ortavant, 1975b; Lincoln & Short, 1980) and the ewe (Legan, Karsch & Foster, 1977), photoperiodically controlled changes in the system governing the tonic mode of gonadotrophin secretion appear to be responsible for the seasonal transitions between reproductive activity and quiescence. During the breeding season tonic gonadotrophin secretion is high; in the non-breeding season it is low. In the male, these changes most probably provide a direct drive to the seasonal fluctuations in testicular function. In the female, however, the changes in tonic gonadotrophin secretion must operate via the luteinizing hormone (LH) surge system to cause the termination and re-initiation of oestrous cycles. More specifically, it has been proposed that oestrous cycles can occur only when tonic secretion of LH is sufficient to stimulate an oestradiol rise which is needed to induce the preovulatory LH surge. Ovarian cycles cease when tonic LH secretion is low because levels of the gonadotrophin are insufficient to produce the oestradiol signal for the LH surge (Legan *et al.*, 1977). Details of this hypothesis and supporting evidence have been described by Legan & Karsch (1979) and Goodman & Karsch (1980).

Although seasonal changes in tonic gonadotrophin secretion appear to be a critical element in both sexes, there is not general agreement as to how they are produced. In the ewe, the seasonal variation in tonic LH secretion is thought to reflect a change in responsiveness to the inhibitory feedback action of oestradiol. In the breeding season oestradiol is a weak inhibitory steroid whereas in anoestrus it is extremely potent in this regard (Legan *et al.*, 1977). In contrast, it has been proposed that seasonal changes in LH secretion in the ram may not require sex-steroid feedback (Lincoln & Short, 1980). This question regarding the importance of sex-steroid feedback is not confined to the sheep. Indeed, it has been raised for numerous other seasonal breeders particularly birds (Follett, 1978) and hamsters (Turek & Campbell, 1979).

Our interest in the importance of steroid feedback has arisen, in part, because the question of steroid dependency touches upon the fundamental mechanisms underlying the photoperiodic

control of reproductive function. If seasonal changes in gonadotrophin secretion do not require sex-steroid feedback, then photoperiod could exert its ultimate influence independently of any steroid-response apparatus, for example by impinging directly upon the process of synthesis and release of gonadotrophin-releasing hormone (GnRH) from endocrine neurones in the hypothalamus (Text-fig. 1a). In this case, apparent changes in response to steroid feedback may merely reflect amplification of another effect. On the other hand, if the change in gonadotrophin secretion requires steroid feedback, then photoperiod could ultimately evoke its action via the steroid-response apparatus, for example by altering steroid receptors within the neuroendocrine axis (Text-fig. 1b). These two hypothetical situations need not be mutually exclusive.



Text-fig. 1. Two general mechanisms for the photoperiodic control of tonic gonadotrophin secretion. (a) Photoperiod directly alters release rate of GnRH and/or gonadotrophin while negative feedback centres for steroids are unaffected. (b) Photoperiod affects response of neuroendocrine axis to steroid feedback and thus indirectly alters the release rate of GnRH and/or gonadotrophins. These two hypothetical situations are not mutually exclusive and neither of them requires separate populations of cells for the actions of steroids and the ultimate effects of photoperiod.

In light of these considerations, it becomes particularly important to evaluate the experimental approaches used to determine whether or not seasonal changes in gonadotrophin secretion require steroid feedback. In this paper, we will examine the data currently available for the sheep and compare the results and conclusions obtained for this species with those obtained for other seasonal breeders.

At the outset a few terms must be defined. Some animals breed in long photoperiods (e.g. birds) while others do so in short photoperiods (e.g. sheep). To avoid confusion when considering the effects of artificial lighting regimens in different species, we will consider photoperiods which lead to the breeding season to be 'stimulatory' and those that lead to the non-breeding condition to be 'inhibitory'. Our usage of this terminology carries no mechanistic implications (i.e. 'stimulatory' photoperiods may actually be non-inhibitory). This designation has its drawbacks, however, as some species can enter a new reproductive state because they become unresponsive ('refractory') to an existing photoperiod. For example, the gonads of photorefractory birds will regress even though they remain under 'stimulatory' photoperiods.

Approaches to study dependency upon steroid feedback

All the methods used to determine whether seasonal changes require steroid feedback involve characterization of circulating LH and/or follicle-stimulating hormone (FSH) in the absence of gonadal steroids. Approaches which have been used include determination of seasonal changes in: (1) the time course of the gonadotrophin increase which follows gonadectomy; (2) average serum gonadotrophin concentrations in long-term gonadectomized animals; and (3) the frequency and amplitude of the acute pulsatile discharges (mainly LH) which occur in gonadectomized animals. We will now examine the results obtained using these approaches, pointing out some advantages and disadvantages of each. However, two important considerations apply to all three approaches.

First, it will be necessary to consider data obtained under natural as well as artificial photoperiods because comprehensive information is not available for either one of them. This necessity raises the possibility that some of the differences observed may result because the responses in artificial photoperiods are not strictly comparable to those under natural conditions in which there are large seasonal swings in a number of other environmental variables.

An even more critical problem concerns the existence of extra-gonadal steroids (adrenal or dietary in origin). A seasonal change in gonadotrophin levels in gonadectomized animals may occur because minute quantities of extra-gonadal steroids act upon an exquisitely sensitive neuroendocrine axis during the non-breeding season. This possibility gains importance in the light of observations that oestradiol implants which produce extremely low oestradiol levels (0.5–1.0 pg/ml) completely suppress LH in ovariectomized anoestrous ewes (R. L. Goodman & F. J. Karsch, unpublished results). Although recent studies suggest that adrenal steroids do not suppress gonadotrophins in hamsters (Ellis & Turek, 1980; Bittman & Goldman, 1979), the importance of these steroids in other species remains to be elucidated. Furthermore, the possible involvement of dietary steroids cannot be completely ruled out because ingestion of oestrogenic clover alters serum LH concentrations in ovariectomized ewes (Hearnshaw, Cumming & Goding, 1977) and dietary factors can influence reproductive activity in other animals (Leopold, Erwin, Oh & Browning, 1976; Berger, Sanders, Gardner & Negus, 1977).

Approach 1: Time course of gonadotrophin increase which follows gonadectomy

An assumption which underlies this approach is that the time course of the gonadotrophin increase which follows gonadectomy is independent of gonadal steroid feedback. A distinct advantage of this approach to examining steroid dependency is the ease of measuring the response to a well-defined stimulus, the removal of gonadal steroids.

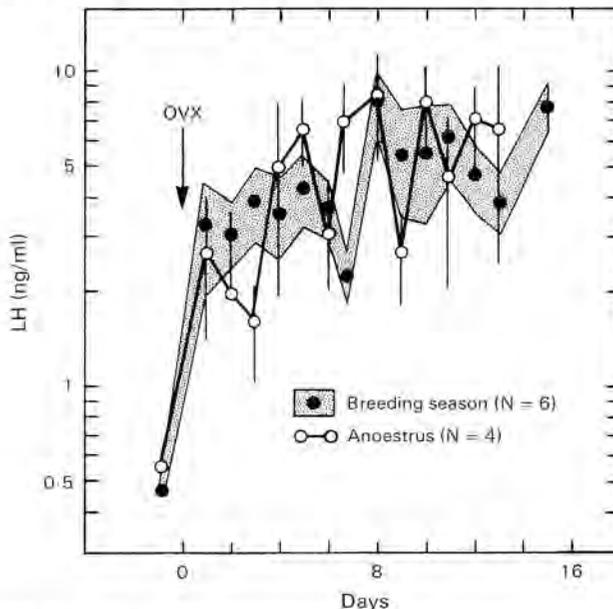
Species other than sheep

The time course of the rise in circulating LH and/or FSH which follows gonadectomy in different artificial photoperiods has been examined in a number of seasonal breeders including the golden hamster, red grouse, tree sparrow, and Japanese quail. In photosensitive birds, the gonadotrophin rise in stimulatory photoperiods is marked and relatively prompt, whereas under inhibitory photoperiods it is attenuated, delayed or even absent as in the Japanese quail (Gibson, Follett & Gledhill, 1975; Davies, Goulden, Follett & Brown, 1976; Wilson & Follett, 1977; Sharp & Moss, 1977). A similar trend is observed in hamsters. In male hamsters, the post-castration rise in FSH is decreased by inhibitory photoperiods while data for LH are contradictory (Turek, Elliott, Alvis & Menaker, 1975; Tamarkin, Hutchison & Goldman, 1976). In females, inhibitory photoperiods produce lower gonadotrophin levels in morning samples taken shortly after ovariectomy. This, however, is complicated by the dramatic increase in levels

of LH and FSH observed in afternoon samples collected under inhibitory photoperiods (Bridges & Goldman, 1975; Bittman & Goldman, 1979). The latter is thought to represent a daily expression of the surge mode of gonadotrophin secretion and this may reduce the ability of the hypothalamo-hypophysial axis to secrete LH and FSH at other times of the day.

Sheep

The time course of the response to castration has been characterized in Soay rams, a primitive breed which inhabits St Kilda, an island in northwest Scotland (Lincoln & Short, 1980). In this breed, LH increases markedly following castration during the non-breeding season, but this rise is both delayed and attenuated relative to that observed in the breeding season (artificial photoperiods). In ewes, the response to ovariectomy has been examined only in the more domesticated breeds and in natural photoperiods. In contrast to findings in the Soay ram, Roche (1969) observed no seasonal difference in the rate or extent of the LH rise which follows gonadectomy of white-face crossbred ewes (Text-fig. 2), a finding we have confirmed with ewes of the Suffolk breed (F. J. Karsch, unpublished data).



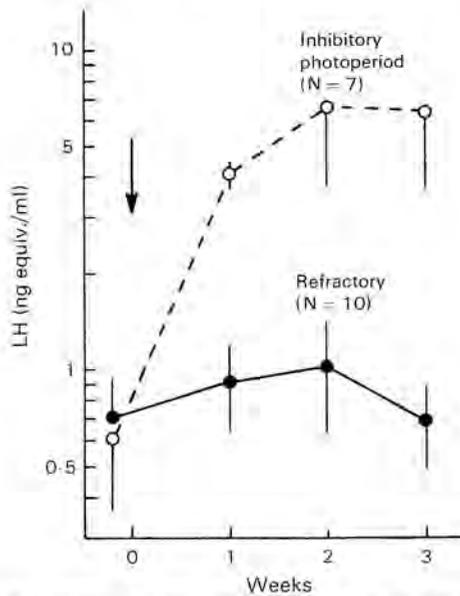
Text-fig. 2. Increase in serum LH concentrations following ovariectomy of white-face crossbred ewes (arrow). The ewes were maintained outdoors in natural photoperiod and ovariectomized during the breeding season or during anoestrus. Values are mean \pm s.e.m. for the no. of ewes indicated. The response to ovariectomy is not affected by season. Adapted from Roche (1969).

Interpretation and evaluation

One obvious interpretation of these findings is that there are species, breed and/or sex differences in the extent to which season (photoperiod) can modify gonadotrophin secretion in the absence of steroid feedback. This produces a spectrum of responses. At one extreme is the Japanese quail in which photoperiod strongly influences gonadotrophin secretion in the absence of gonadal hormones. At the other extreme lies the domestic ewe in which seasonal changes in tonic gonadotrophin secretion fail to occur in the absence of gonadal feedback. Between these two extremes lie other birds, the hamster, and the Soay ram.

Such a conclusion, however, is subject to many reservations. For example, the response to

gonadectomy in a given reproductive state may be grossly different depending on the reason for being at that state. A good example of this comes from the canary which can have seasonally regressed gonads because it is in an inhibitory photoperiod or is refractory to a stimulatory photoperiod. In either sex, LH increases markedly following gonadectomy if gonadal regression is due to inhibitory photoperiods, whereas LH does not increase if gonadal regression is due to photofractoriness (Text-fig. 3) (Hinde, Steel & Follett, 1974; Nicholls & Storey, 1976). It should be noted that this dichotomy between photorefractory and photosensitive animals does not occur in all species (Sharp & Moss, 1977; Ellis, Losee & Turek, 1979). Nonetheless, the observations in the canary must serve as a warning for our interpretation of findings in other species, particularly those like the sheep in which the condition of photorefractoriness, if it exists, remains to be characterized.

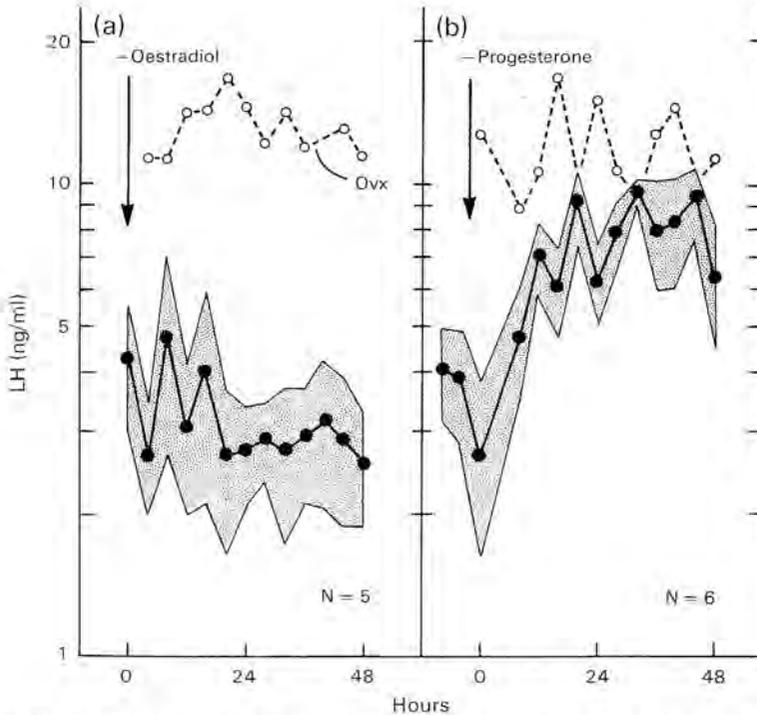


Text-fig. 3. Mean (\pm s.e.m.) concentrations of serum LH after castration (arrow) of photo-refractory and photosensitive canaries with regressed gonads. The photorefractory birds had been exposed to a stimulatory photoperiod for 3–5 weeks after spontaneous testicular regression. In photosensitive birds, refractoriness had been 'broken' by exposure to inhibitory photoperiods for 10 weeks after spontaneous testicular regression. Adapted from Nicholls & Storey (1976).

Perhaps a more fundamental limitation to this approach is that the time course of the gonadotrophin rise which follows gonadectomy may be influenced by the degree of suppression of the hypothalamo–hypophysial–gonadal axis before surgery. For example, it has been argued that a decreased suppression of gonadotrophin by sex-steroid feedback in the breeding season would lead to a more rapid response (Davies *et al.*, 1976). Conversely, an extreme suppression of the hypothalamus and pituitary by gonadal steroids in the non-breeding season would be expected to result in a sluggish increase in gonadotrophins following removal of the gonads. This point is particularly relevant to those animals, such as the Soay ram, in which LH levels are largely undetectable prior to castration in the non-breeding season (Lincoln & Short, 1980).

Finally, the post-gonadectomy rise in LH and FSH may be influenced by the identity of the inhibitory steroid before surgery. This possibility is illustrated by the observations in Text-fig. 4. Although oestradiol and progesterone produced a similar degree of suppression in ovariectomized Suffolk ewes, their withdrawal did not result in a similar increase in LH. After removing progesterone, LH increased promptly. This rise was delayed after removing oestradiol, and in fact, LH did not rise at all during the 48 h after withdrawal of this steroid. These data force one

to question the assumption that the time course of the gonadotrophin increase which follows gonadectomy is independent of sex-steroid feedback, the premise which underlies this approach. This matter becomes particularly troublesome in view of evidence that the primary inhibitory steroid may vary with season, at least in the ewe (Hauger, Karsch & Foster, 1977; Goodman & Karsch, 1980).



Text-fig. 4. Serum LH concentrations (mean \pm s.e.m.) before and after withdrawal (arrow) of (a) oestradiol or (b) progesterone from ovariectomized Suffolk ewes during the breeding season. Before withdrawal, the steroids had been administered via Silastic (Dow Corning) implants inserted at the time of ovariectomy 2 weeks earlier. The implants maintained physiological serum concentrations of oestradiol (2–4 pg/ml) or progesterone (3–5 ng/ml), and each steroid produced a comparable inhibition of LH. LH increased promptly after removal of the progesterone implants but only after several days (data not shown) in the ewes from which oestradiol was withdrawn. O—O, mean concentration of LH in ovariectomized control ewes.

Because of these reservations, the short-term response to the removal of presumably all negative feedback hormones may not resolve the question of whether seasonal changes in tonic gonadotrophin secretion depend on sex-steroid feedback. Therefore, we must look to results from other approaches.

Approach 2: Serum gonadotrophins in long-term gonadectomized animals

A second approach to examining the issue of steroid dependency has been the determination of circulating LH and/or FSH throughout the year (or in a photoperiodically induced seasonal cycle) in long-term gonadectomized animals. This approach is based on the assumption that

gonadotrophin concentrations in such animals are not influenced by negative feedback hormones. It has the distinct advantage that the concentration of gonadotrophin in the long-term absence of the gonads is not likely to be influenced by the steroidal milieu prior to gonadectomy, a serious limitation of the preceding approach. Thus, any seasonal change which may exist should be independent of sex-steroid feedback.

Species other than sheep

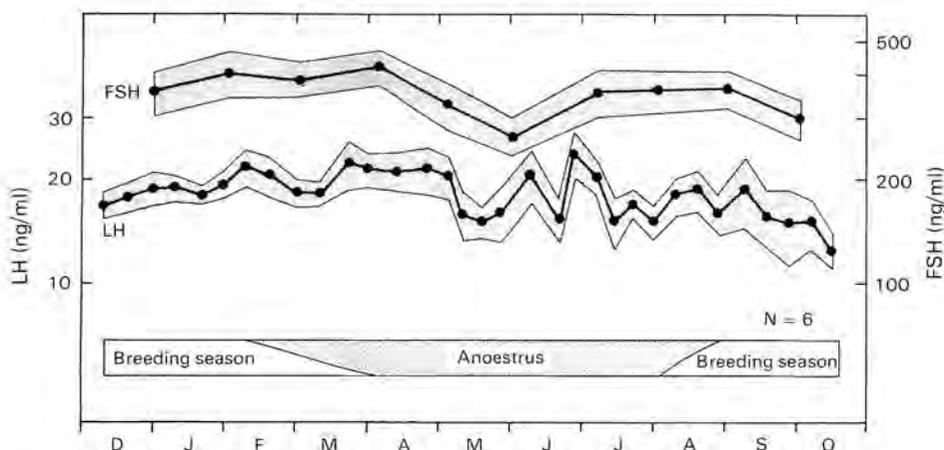
Seasonal changes in LH and/or FSH in the long-term absence of the gonads have been examined in many seasonal breeders including the Japanese quail, red grouse, a variety of sparrows, golden hamsters, snowshoe hares, red deer and ponies. As with the preceding approach, the results differ among species. For example, serum LH concentrations in the breeding season are greater than those in the non-breeding season in gonadectomized pony mares, snowshoe hares, and birds, whereas no seasonal difference is apparent in the red deer stag maintained in natural photoperiod (Davis & Meyer, 1973; Wilson & Follett, 1974; Gibson *et al.*, 1975; Sharp, Moss & Watson, 1975; Garcia & Ginther, 1976; Mattocks, Farner & Follett, 1976; Freedman, Garcia & Ginther, 1979; Lincoln & Kay, 1979). Most, but not all, studies of long-term gonadectomized male hamsters have failed to reveal an effect of photoperiod on the level of LH or FSH (Turek *et al.*, 1975; Turek, 1977; Ellis & Turek, 1979). In ovariectomized female hamsters, however, gonadotrophin levels in the morning are lower in inhibitory photoperiods than in stimulatory ones, but surges are observed in the afternoon (Seegal & Goldman, 1975).

Sheep

The effect of artificial photoperiods on circulating gonadotrophins has been investigated for the long-term castrated Soay ram as well as for the more domesticated Ile-de-France ram. An effect of photoperiod is evident in both breeds, with gonadotrophin concentrations decreasing slightly following exposure to an inhibitory photoperiod (Pelletier & Ortavant, 1975a; Lincoln & Short, 1980). In the Soay rams, however, this decrease was only transitory with gonadotrophin concentrations soon returning to the level seen under a stimulatory photoperiod. In the female, Land, Wheeler & Carr (1976) observed that serum LH did not decrease during the non-breeding season in long-term ovariectomized Scottish Blackface or Finnish Landrace ewes maintained in natural photoperiod. Similarly, we have failed to detect a consistent seasonal change in circulating LH or FSH throughout the year in ovariectomized Suffolk ewes maintained outdoors (Legan *et al.*, 1977; Legan & Karsch, 1981). This was the case whether infrequent observations were made in the same animal throughout the year (Text-fig. 5) or whether samples were obtained every 2–4 hours throughout the day at various times of the year (Karsch, Goodman & Legan, 1980).

Interpretation and evaluation

The results obtained using this approach again suggest that there may be species, breed and/or sex differences in the extent to which seasonal changes in gonadotrophin secretion depend on sex-steroid feedback. Again, the domestic ewe may lie at one end of a spectrum (steroid-dependent), most birds at the other end (steroid-independent), and the Soay ram in the middle. Interestingly, in contrast to the results obtained using the first approach, the male hamster more closely resembles the ewe than it does the Soay ram. As with the previous approach, however, there are a number of reservations which preclude a definitive conclusion. For example, we cannot discount ambiguities arising from the possible existence of



Text-fig. 5. Mean (\pm s.e.m.) serum concentrations of LH and FSH throughout the year in 6 ovariectomized ewes (mixed breeds). The ewes were maintained outdoors under natural environmental conditions. The occurrence of the breeding season in ovary-intact ewes maintained together with the ovariectomized ewes is depicted by the horizontal bar. LH data from Legan *et al.* (1977); FSH data from Legan & Karsch (1980).

photorefractory states and, in fact, the phenomenon of refractoriness has been invoked to explain the transitory nature of the response to inhibitory photoperiod in the Soay ram (Lincoln & Short, 1980).

The use of long-term gonadectomized animals, while overcoming a major disadvantage of the first approach, introduces another set of problems. Foremost among these is the fact that the response of the neuroendocrine axis to steroidal inhibition changes markedly as a function of time after gonadectomy (Brown, Cumming, Goding & Hearnshaw, 1972; Karsch, Weick, Hotchkiss, Dierschke & Knobil, 1973; Karsch, Legan, Hauger & Foster, 1977). This exacerbates the potential problem of extra-gonadal steroids and raises the possibility that the effectiveness of other inhibitory inputs, such as photoperiod, may also be altered after removal of the gonads. The latter point is especially pertinent to those species in which no seasonal difference in gonadotrophin was observed (e.g. ewe, stag). Specifically, it may be argued that the stimulus to secrete gonadotrophins is so very great in the chronic absence of sex steroids that it masks any direct influence of photoperiod. For example, the stimulus to the GnRH-producing neurones may already be supramaximal in the absence of steroids, even under an inhibitory photoperiod, such that a further drive resulting from a transfer to a stimulatory photoperiod has no effect.

One additional limitation to the use of long-term gonadectomized animals concerns the extensive variability in circulating gonadotrophins characteristic of this condition. This variability, which is produced by large pulsatile releases of hormones (especially LH; Dierschke, Bhattacharya, Atkinson & Knobil, 1970; Butler, Malven, Willett & Bolt, 1972), can make it difficult to obtain an adequate assessment of gonadotrophin levels if only a small number of samples is collected, as in the study of Pelletier & Ortavant (1975a) on Ile-de-France rams. This becomes particularly troublesome if the seasonal difference is small or non-existent, and if the animal studied is not large enough to permit the collection of frequent blood samples.

In addition to increasing variability, the pulsatile pattern of gonadotrophin secretion introduces an important new dimension to our consideration of whether seasonal changes in tonic gonadotrophin secretion require steroid feedback. Perhaps there are seasonal changes in characteristics of the individual pulses of hormone secretion, changes which are not disclosed when observations are made infrequently and data are presented as group means.

Approach 3: Frequency and amplitude of pulsatile gonadotrophin discharges in gonadectomized animals

To understand the rationale for this approach, it is necessary to digress briefly and consider the role of pulsatile gonadotrophin secretion in the control of seasonal breeding. In both the intact red-deer stag (Lincoln & Kay, 1979) and Soay ram (Lincoln, Peet & Cunningham, 1977; Lincoln & Peet, 1977), the increase in gonadotrophin secretion associated with a shift from inhibitory to stimulatory photoperiods results primarily from an increase in the frequency of gonadotrophin pulses. In intact ewes LH pulses occur only occasionally during anoestrus, but are frequent during the preovulatory period of the oestrous cycle (Scaramuzzi & Baird, 1977; Yuthasastrakosol, Palmer & Howland, 1977; Baird, 1978). Such observations suggest that photoperiod may regulate reproductive function primarily by modulating the frequency of gonadotrophin discharges (Lincoln & Short, 1980). If this is the case, then the question of steroid dependency can be addressed by determining if inhibitory photoperiods decrease pulse frequency in long-term gonadectomized animals. This approach is particularly relevant in those animals in which seasonal changes in gonadotrophin secretion were not demonstrable with Approaches 1 and 2. In these animals, there may have been reciprocal and offsetting seasonal changes in the frequency and amplitude of gonadotrophin pulses without corresponding differences in the mean level. Information pertaining to this possibility is scant and available only for LH.

Species other than sheep

The pattern of LH pulses in different seasons has been examined for the castrated male red deer housed indoors but exposed to natural fluctuations in photoperiod (Lincoln & Kay, 1979). No obvious and consistent seasonal change in either the frequency or amplitude of LH pulses was observed on 6 different occasions throughout the year.

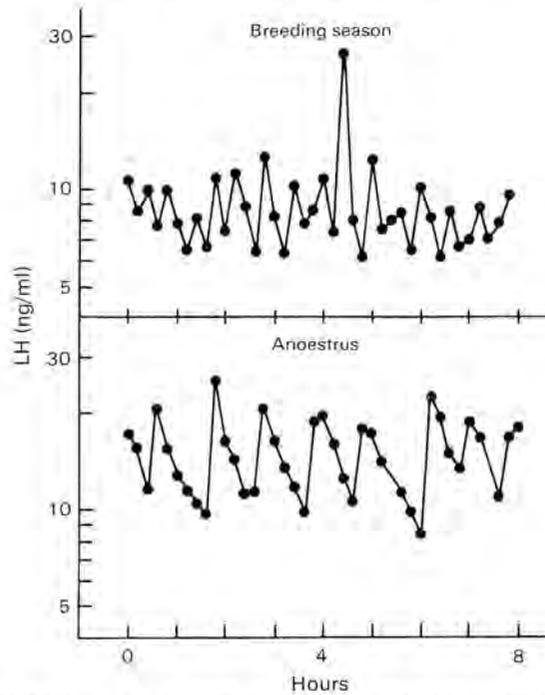
Sheep

In males, the pulsatile pattern of LH secretion has been examined during the first 15 days after castration for Soay rams maintained in stimulatory or inhibitory photoperiods (Lincoln & Short, 1980). Due to the sluggish response under the latter conditions (see Approach 1), unambiguous LH pulses were evident only on Day 15. At that time, however, there was no obvious difference in either the frequency or amplitude of LH pulses as compared to those on Day 15 after orchidectomy under stimulatory photoperiods.

In contrast, we have observed a seasonal difference in Suffolk ewes maintained outdoors when LH pulses were examined on Day 10 after ovariectomy: the amplitude of the LH pulse was greater in anoestrus whereas the frequency tended to be greater in the breeding season, although the latter was not statistically significant (Karsch *et al.*, 1980). In a study currently in progress, we are re-examining the effect of season on LH pulses in the ewe, this time in the long-term absence of the gonads in an attempt to accentuate a possible seasonal difference. Preliminary results reinforce the view that the LH-pulse pattern changes with season under these conditions. Large, well-organized pulses occurred at hourly intervals in anoestrus whereas more frequent, lower amplitude pulses prevailed in the breeding season (Text-fig. 6).

Interpretation and evaluation

These results provide the first suggestion that some seasonal difference in gonadotrophin secretion may occur without gonadal feedback in the ewe, an animal for which Approaches 1 and 2 failed to reveal any such change. In addition, they suggest that a fairly specific change in



Text-fig. 6. Concentrations of LH in samples of serum obtained every 12 min from long-term ovariectomized Suffolk ewes maintained outdoors. Data are from one representative individual during the middle of the breeding season (December) and in mid-anoestrus (June).

hypothalamic function may underlie the photoperiodic control of seasonal breeding. Since LH pulses are most likely to be produced by episodic discharges of GnRH from hypothalamic neurones (Carmel, Araki & Ferin, 1976; Belchetz, Plant, Nakai, Keogh & Knobil, 1978; Lincoln & Short, 1980), the seasonal differences in LH-pulse frequency may reflect an effect of photoperiod on the neural mechanisms which control the interval between GnRH discharges. The explanation for the reciprocal changes in LH-pulse amplitude is more difficult. This could be due to a photoperiodic effect on the amount of GnRH released in each discharge. On the other hand, amplitude changes may be secondary to the modification of frequency; for example less hormone (LH or GnRH) may be available for release when discharges are rapid.

The interpretation of these results is beset with virtually all the reservations discussed for Approach 2. Further, it must be recognized that a description of pulsatile LH secretion provides but a 'keyhole' through which one can obtain a highly detailed view of LH secretory dynamics. The expanse of this view is, by necessity, extremely limited. The observations, therefore, may not adequately represent a given reproductive state or even the secretory dynamics throughout a 24-h period on a single day of one reproductive state. Finally, it should be emphasized that the importance of changes in frequency of LH pulses to an animal's seasonal reproductive status is, at this time, somewhat speculative. One cannot rule out the possibility that changes in average serum gonadotrophin levels are critical, regardless of whether these are produced by changes in pulse frequency or amplitude.

Conclusion

Although the matter of whether or not seasonal changes in tonic gonadotrophin secretion require sex-steroid feedback might initially seem rather straightforward, a thorough evaluation of the available evidence reveals that any conclusions must be extremely tentative. We are especially

reluctant to choose between the possible mechanisms for the photoperiodically induced changes in tonic gonadotrophin secretion (Text-fig. 1) because of the problem of extra-gonadal steroids. This point is underscored by the example of photorefractory canaries and tree sparrows, in which data based on Approaches 1 (Text-fig. 3) and 2 lead to the conclusion that steroid feedback plays no role (Hinde *et al.*, 1974; Wilson & Follett, 1974; Nicholls & Storey, 1976). Despite these compelling data, this conclusion may be questioned in light of the observation that intracranial implantation of anti-androgen blocks gonadal regression in photorefractory sparrows (Cusick & Wilson, 1972). One is on much safer ground, however, in drawing definitive conclusions as to the importance of gonadal steroid feedback and we will therefore limit our considerations to steroids from this source.

In this report, we have tended to emphasize the differences in the importance of steroid feedback amongst different species, breeds and/or sexes, but we should not overlook the similarities. In all types of animals studied, there is now evidence for effects of photoperiod on tonic gonadotrophin secretion independent of the feedback of gonadal steroids. On the other hand, with the possible exception of certain birds, all species show an increase in circulating gonadotrophins when regressed gonads are removed. Further, seasonal changes in response to sex-steroids have been demonstrated in every species examined to date, including Japanese quail (Davies *et al.*, 1976), hamsters (Tamarkin *et al.*, 1976; Ellis & Turek, 1979) and Ile-de-France rams (Pelletier & Ortavant, 1975b), and Suffolk ewes (Legan *et al.*, 1977). Steroid-dependent and steroid-independent changes in tonic gonadotrophin secretion both appear to play a role in most, if not all, seasonal breeders.

Within this broad overview, there emerges a spectrum of species based on the relative degree of steroid dependency. At one end are most birds in which steroid-independent changes in tonic gonadotrophin secretion predominate; in the middle are hamsters and the Soay ram; and at the other end is the domestic ewe, which appears to rely primarily on steroid-dependent changes. It is tempting to speculate that the degree of steroid dependency may relate to the degree of gonadal regression during the non-breeding season. In those animals in which gonadal function appears to collapse almost totally (e.g. birds), a steroid-independent suppression of the neuroendocrine axis may prevail because gonadotrophin secretion remains low despite the presence of apparently non-functional gonads. On the other hand, the dependence on gonadal steroids in the domestic ewe may ensure that many aspects of ovarian function (e.g. follicular development) are not markedly suppressed in anoestrus.

Based on the studies described in this review, we favour the conclusion that the differences between the Soay ram and the Suffolk ewe are due to breed rather than sex differences. In particular, this difference may reflect the relative degrees of domestication of these two breeds. Prolonged association with man may have produced, in the Suffolk, an animal that is in transition from being a strongly seasonal breeder (as is the Soay) to a completely non-seasonal breeder. Further, the shift from steroid-independent to steroid-dependent control of tonic gonadotrophin secretion may be one mechanism underlying this transition. Finally, these considerations raise the possibility that differences in seasonal reproductive patterns among farm animals could be accounted for, in part, by the extent to which they have been domesticated.

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