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Endocrine and Physiological Responses of the Female Goat During Three Reproductive Phases

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ENDOCRINE AND PHYSIOLOGICAL RESPONSES OF THE FEMALE GOAT DURING THREE REPRODUCTIVE PHASES

by

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Dana Dean Clark

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ABSTRACT

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by

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Female Spanish x Dairy cross goats were divided into three reproductive phases--breeding season or cyclic (20), seasonal anestrus (20), and early postpartum (20). Each group of animals was further divided into three treatments--control (10), Gonadotropin Releasing Hormone (GnRH) treated (5), and pituitary Luteinizing Hormone (LH) (5). During each of the above mentioned reproductive phases, the following were measured: progesterone and LH profiles, serum LH levels following GnRH injection, pituitary LH concentration and ovarian responses following GnRH treatment.

Progesterone levels indicative of luteal development were present only in the breeding season. Progesterone levels during the seasonal anestrous and postpartum periods were 0.65 ± 0.03 and 0.30 ± 0.02 ng/ml, respectively, and significantly different ($P < 0.01$).

The LH surge mechanism was operational only in breeding season does, showing LH peaks of 187.86 ± 3.95 ng/ml an average of 13.2 ± 1.47 hours after the onset of estrus. LH levels returned to 2 ng/ml by 48 hours post estrus. There was an inverse relationship between plasma progesterone and LH with mean LH levels of 1.1 ± 0.13 ng/ml during the luteal phase of the cycle. Serum LH levels during the seasonal anestrous and postpartum period were 0.71 ± 0.02 and 0.32 ± 0.02 ng/ml, respectively. These differences in tonic LH secretion were significant.

Tonic LH levels (0.5 ± 0.2 ng/ml) were recorded in all does, regardless of the reproductive phase, prior to the initial injection of GnRH. Serum LH increased to 182.96 ± 54.56, 209.38 ± 41.38, and 97.84 ± 55.84 ng/ml, these peak levels were recorded at 114 ± 4, 135 ± 7, and 135 ± 11 minutes post injection in cyclic, seasonal anestrous, and postpartum does, respectively. Response to the second injection was more rapid and heightened, peaks were achieved from 27 ± 3 to 66 ± 14 minutes post injection, LH peak levels were higher than those recorded following the first injection. Postpartum animals showed reduced responses in all cases.

Pituitary LH concentrations were 1711 ± 378, 2069 ± 265, and 3542 ± 398 ug LH/g tissue in the postpartum, seasonal anestrous, and cyclic animals, respectively. Because of high nonspecific binding, these concentrations are considered as estimates, nevertheless, trends observed are considered to be real.

GnRH was effective in inducing ovarian activity in seasonal anestrous and cyclic does, no such response was noted in postpartum animals.

(97 pages)

INTRODUCTION

The goat is an important source of food and fiber throughout the world. Available data collected in 1974 (FAO, 1975) indicate that in many Asian and African countries, goat milk comprises over 20 percent of the total milk produced. Goat meat accounts for approximately 5.7 percent of the world production of edible protein (FAO, 1976). This value is no doubt a gross underestimate since most goats are slaughtered and consumed at the village level, unrecorded by national statistics (Sands and McDowell, 1979). Geographically at least two thirds of the total goat population is located within 30 degrees of the equator where they make a significant contribution to food resources in underdeveloped countries, "thus the value of the goat and its contribution to human welfare is greater than is indicated by statistical figures because their products fill a greater need" (Shelton, 1978, p. 994).

Many of the attributes of the goat distinguish them as a useful and efficient animal. Goats have a limited subcutaneous fat covering, and a relatively small size to surface area ratio, which makes them very adaptable to regions of high ambient temperature (Shelton, 1978). Their small size relative to the cow makes them desirable in smallholder agricultural systems. Nutritional requirements of goats are comparable to cattle and sheep, however, goats are superior to other ruminants in their ability to digest low

protein, high roughage diets (Louca et al., 1982). This quality, bestows upon the goat the ability to utilize a wide variety of vegetation, much of which cannot be utilized by other domestic species (Macfarlane and Howard, 1972). There have been claims made that the goat is a more efficient milk producer, as compared to other species. Available data summarized by Devendra (1975) would seem to substantiate these claims. In more affluent societies, interest in the dairy goat is rapidly increasing because of the special health qualities attributed to goat's milk, and the general "back to the farm" movement. Interest in the goat as an animal model in the study of ruminant physiology and biomedical research is increasing (Hoversland, et al, 1965; Shelton, 1978).

Unfortunately, in light of the significant contributions of food and fiber made by the goat and the vital niche its products fill in underdeveloped countries, relatively very little research has been conducted on this animal. Reproduction is a major contributing factor to efficiency in goat production. Research directed toward understanding the endocrinology of reproduction in goats has been minimal to date, especially in view of this animal's potential for increased production.

Objectives

A. To define specific endocrine and physiological characteristics of the female goat during selected periods of the breeding season, seasonal anestrus, and early postpartum period. This will be achieved by measuring the following:

1. Progesterone and Luteinizing Hormone (LH) profiles.
2. LH concentrations in the anterior pituitary.
3. Estrous cycle length and ovarian activity.

B. To determine the anterior pituitary and ovarian responses of the doe, at selected periods of the breeding season, seasonal anestrus, and early postpartum period, to a selected level of Gonadotropin Releasing Hormone (GnRH). The following measurements will be taken:

1. Plasma LH levels following administration of GnRH.
2. Ovarian activity following GnRH administration.

Achievement of these objectives provide clues into the operation of the nervous and endocrine system and their interaction with environmental factors, as they relate to reproduction. In addition, these data provide a base from which research may be designed to obtain more detailed and definitive information on the endocrinology of seasonal and postpartum anestrus in the goat.

REVIEW OF LITERATURE

General Reproductive Parameters of the Goat

The yearly reproductive cycle of the goat (excluding the gestation and postpartum periods) consists of a breeding and nonbreeding (seasonal anestrus) season. This seasonal cycle in reproductive activity is regulated primarily by changes in photoperiod (Bissonnette, 1941; Hafez, 1952; Godley et al., 1966; Shelton and Spiller, 1977; Ortavant, 1977; Turek and Campbell, 1979). The male as well as the female goat exhibit a seasonal cycle in reproductive activity (Shelton, 1978; Muduuli, 1978). Under this condition the breeding season begins in early fall and extends until late winter when the increasing day length signals the animal to begin the anestrous season; anestrus continues until the resumption of estrous cycles in late summer or early fall. Some breeds of goats, particularly near the equator where changes in photoperiod are minimal, do not exhibit a seasonal anestrous period rather they show year-around sexual receptivity (Hafez, 1974). Taking the sheep as an example, breeds which evolved and are near the equator are expected to show less response to the photoperiod; and seasonal restrictions, if they are exhibited, may be explained by other elements of the environment such as feed supply or humidity (Mishra and Biswas, 1966). By contrast, breeds which originate and are located in more temperate regions show considerable seasonality in reproductive activity.

The length of the estrous cycle is from 18 to 24 days with a mean of approximately 20 days (Corteel, 1977; Carrera and Butterworth, 1968; Kakusya, 1979; Thornburn and Schneider, 1972; Shelton, 1960). Romm, in 1977-78, working with goats at Utah State University found the mean estrous cycle length to be 20.32 ± 7.12 days. Riera (1982) in his review of reproduction in goats, reported that the majority of estrous cycles are 19-21 days in length, with a significant degree of variation between animals. Utilizing the records of 1,099 estrous cycles Prasad and Bhattacharyya (1979) categorized the estrous cycle lengths as short, medium, and long. The frequency of each category was 19.7, 68.8, and 11.5 percent and 6.4, 19.8, and 37.5 days of duration, respectively. The overall mean was 19.2 days.

The length of estrus appears to be highly variable, this large variability may more nearly represent differences in interpretation since estrus is difficult to define. Carrera and Butterworth reported estrus to be 34.4 ± 8.1 hours, while Van Rensburg (1964) reported 22 hours for the Angora breed. In their review of the goat as a meat producer, McDowell and Bove (1977), stated 40 hours as the average duration of estrus with standing estrus lasting 12 to 24 hours. Shelton (1978) stated that 36 hours is the most commonly stated value for the length of the estrous period.

Ovulation generally is reported as occurring a few hours after the termination of standing heat (Shelton, 1978). Jaroz et al. (1971) using laparoscopic techniques observed ovulation 4.23 ± 0.25, 3.1 ± 0.18, and 2.11 ± 0.16 days after the appearance of behavioral estrus in the Toggenburg, Pygmy, and crossbred (Pygmy 7/8) breeds of goat,

respectively. Kakusya (1979) postulates the interval from the onset of estrus to ovulation in the Pygmy to be between 36 and 48 hours. In the ewe, ovulation occurs approximately 24 hours after the onset of estrus (McKenzie and Terrill, 1937).

Relatively little data on ovulation rate has been reported in the literature (Shelton, 1978). Recently Rao and Bhattacharyya (1980) observed an average of four ovulation points 48 hours after the onset of estrus in the Black Bengal breed. Other researchers have reported mean ovulation rates during the breeding season in the Angora, Barbari, and non-descript Indian goats of 1.2, 1.43, and 1.07 ovulations/doe, respectively (Shelton, 1960; Bhattacharyya and Prasad, 1974; Basu et al., 1961).

Research on goats and sheep indicate a strong correlation between body weight and age at the first expression of puberty (Epstein and Hertz, 1964; Williams, 1954; Keane, 1974; Shelton, 1978). Body weight is dependent upon many factors such as the level of nutrition, age, type of birth, and the season of year the kids are born. Riera (1982) reviewed the literature available on puberty in the goat, and reported most breeds to be pubertal between five and 10 months of age. Considerable difference has been shown in the age of the attainment of puberty among genotypes (Yao and Eaton, 1954; Rogers et al., 1969; McDowell and and Bove, 1977; Rahman et al., 1977). Caution must be exercised in interpreting data comparing the age of attainment of puberty among genotypes since some degree of variability in the age at puberty may be accounted for by differences in environment and management conditions under which the animals were raised.

The expression of puberty is inhibited by the photoperiod in both sheep and goats (Amoah and Bryant, 1980; Wiggins et al., 1970; Foster, 1981). It has been shown that those animals attaining pubertal age and size during the period of seasonal anestrus will not exhibit estrus until the photoperiod permits reproductive activity.

The average gestation period of the goat has been reported in the literature to vary from 144 to 150.8 days with a mean of 149 days (Riera, 1982; Shelton, 1961; Van Rensburg, 1964). Shelton (1978) in his review of reproduction in goats stated that a mean gestational length of 149 days appears to be standard throughout most breeds with one exception noted, that of the Black Bengal breed whose mean gestation length was 143 days (Ali et al., 1975).

Reproductive Hormone Levels During Selected Reproductive Phases

Introduction

During the breeding season, or at a time when environmental factors are conducive to reproductive cyclicity in the female goat, the estrous cycle is principally regulated through the interactions of steroid hormones secreted primarily by the ovary and the protein gonadotropins of the anterior pituitary. The hypothalamus acts as a vital link between the nervous and endocrine systems, particularly in controlling the secretions of the anterior pituitary. Uterine secretions also participate in the chain of hormonal events which control the estrous and ovarian cycles (Goding et al., 1971-72).

The organization of a typical 20 day estrous cycle may be divided into a 3-4 day follicular phase and a 15-17 day luteal phase.

Relatively high levels of progesterone are characteristic of the luteal phase. The pattern of progesterone secretion is reflected by the growth and subsequent regression of the corpus luteum, which is governed by stimulatory factors from the pituitary and inhibitory factors from the uterus (Nalbondov, 1973; Hansel et al., 1973; Goding 1974). Ovarian follicles, which are stimulated to develop by pituitary gonadotropins, are the major source of serum estradiol levels. Two separate regulatory systems govern the secretion of gonadotropins from the anterior pituitary, a tonic system, producing relatively low pulsatile discharges of gonadotropins during most of the cycle and a surge system which generates a massive preovulatory surge of gonadotropins (Goding et al., 1970; Scaramuzzi et al., 1971; Foster et al., 1975; Hauger et al., 1977; Legan and Karsch, 1979). Foster and Karsch (1976) demonstrated that luteal levels of progesterone can exert a potent inhibition of tonic LH secretion in the ewe, this effect seems to be enhanced by basal levels of estradiol. In 1979, Kakusya noted this same relationship held true in the goat. The culmination of the follicular phase is behavioral estrus and ovulation, which is the physical manifestation of the hormonal milieu at this stage characterized by high estrogen levels and the LH surge.

Because of the common ancestry of the sheep and goat, many physiologic and endocrine phenomena are assumed to be similar and in many cases have been proven similar. Nevertheless, some significant differences do occur. During pregnancy, the sheep and goat differ markedly in the way they synthesize progesterone (Linzell and Heap, 1968) to maintain pregnancy. Removal of the corpus luteum after

approximately 50 days gestation in the sheep will not result in abortion because the placenta has replaced the corpus luteum as the major progesterone source. The goat, on the other hand, is dependent on the corpus luteum to maintain pregnancy throughout gestation. Data collected to date suggests that the events of the estrous cycle in sheep and goats are similar, nevertheless, extrapolation of sheep data to explain reproductive phenomena in the goat is not always valid and this fact must be kept in mind when comparing endocrine profiles of these two species.

Reproductive hormone levels during the breeding season

Kakusya (1979) using a Radioimmunoassay (RIA) technique reported progesterone levels of female Pygmy goats during the breeding season. He observed basal levels (mean ± SEM of 0.7 ± 0.007 ng/ml) on day 0, by day 3 they began to increase rapidly reaching maximal values by day 9 (9.3 ± 0.3 ng/ml, range of 7.2 to 12.2 ng/ml). Progesterone levels remained high at approximately the maximal mean from day 9 to day 15. Beginning on day 16 or 17 of the cycle (day -2 or -3 of the upcoming cycle) a precipitous decline was observed to the minimal values observed at day 0.

Romm (1979) reported progesterone levels of Spanish x Dairy cross goats following the same pattern as previously reported by Kakusya. At the time of estrus, basal progesterone levels were 0.2 ng/ml, thereafter increasing to 6.0 ng/ml by day 10. She reported further that progesterone levels began a precipitous decline on day -2 of the cycle.

Research conducted by Wentzel et al. (1979) reported caprine progesterone levels of 0.4 ng/ml at estrus, increasing gradually to 6.7 ng/ml by day 13. This maximal level was maintained until three days before the start of the next cycle when it decreased abruptly.

Jones and Knifton (1972) found progesterone secretion during the goat estrous cycle to follow the same pattern as reported by other researchers but the maximal levels in mid-luteal phase were higher than previously reported (approximately 16 ng/ml). A competitive protein binding assay was used in the analysis.

Luteinizing hormone (LH) in the normally cycling goat have been measured by two investigators, Kakusya (1979) and Romm (1979).

Kakusya sampled two mature female goats at 20 minute intervals for 24 hours during several different reproductive phases including the breeding season. His findings demonstrate that LH secretion in the goat is pulsatile, with the frequency of pulses being related to the stage of the estrous cycle. In mid-luteal phase, the LH pulses were less frequent with peak pulse levels of approximately 2.0 ng/ml while samples taken in the follicular phase yielded as high as 11 pulses in a 24 hours period with a mean peak pulse level of 3.8 ng/ml. These results agree with similar studies using the ewe in that the time between pulses decreases during the follicular phase (Yuthasastrakasol et al., 1975). However, they differ in the respect that more frequent pulses have heretofore been associated with lower pulse peak values (Cicmanic and Niswender, 1973; Yuthasastrakasol et al., 1975). These results support those obtained in the ewe by Karsch et al. (1977) suggesting that luteal levels of progesterone suppress the tonic LH

pulse frequency.

Kakusya (1979) also measured the mean peripheral plasma levels daily throughout the breeding season. LH mean concentrations peaked at day 0 (11.4 ± 1.2, range 6.5 to 21.5 ng/ml) and returned to baseline values (0.3 ± 0.1 ng/ml) by day 3 of the cycle.

Using RIA techniques and sampling every six hours for 48 hours following detection of estrus and thereafter one time each day, Romm (1979) measured plasma LH levels and found an inverse relationship between LH and progesterone levels with LH concentrations increasing slightly from day -3 to the day of estrus. LH peaks of >200 ng/ml were observed in 8 of the 10 goats an average of 24.0 ± 8.94 hours after the onset of estrus. While LH levels in mid-luteal phase were an average of approximately 1.0 ng/ml.

Reproduction hormone levels during the period of seasonal anestrus and transition into and out of breeding activity

Progesterone levels in the goat during the seasonal anestrous period were reported in 1972 by Jones and Knifton, observing a mean progesterone concentration in the peripheral plasma of 0.8 ± 0.28 ng/ml. The progesterone levels fluctuated narrowly around these low levels throughout the anestrous period.

Kakusya (1979) found progesterone levels fluctuating at low levels (approximately 0.5 ng/ml) throughout anestrus. An approximate four-fold increase in progesterone levels occurred two days before the first ovulation in the transition into the breeding season. They then declined to baseline values on the day of the first ovulation. Following ovulation, a typical breeding season profile was observed.

The frequency of LH pulses during the seasonal anestrous period were observed to decrease to approximately 3 to 4 pulses in a 24 hour period (as compared to an average of 8 pulses/24 hours during the breeding season) but these less frequent episodic pulses were shown to have slightly higher values than those of the more frequent pulses of the breeding season (6.7 $\pm$ 0.3 and 5.6 $\pm$ 0.4 ng/ml vs. 3.4 $\pm$ 0.3 and 4.2 $\pm$ 0.3 ng/ml for goats #5353 and #5151, respectively) (Kakusya, 1979). No preovulatory LH surge concentrations were noted in the peripheral plasma during the seasonal anestrous period.

Two investigators have measured reproductive hormone levels in the ewe during the seasonal anestrous period and transition into breeding activity.

Walton et al. (1977) using RIA techniques measured LH, Follicle Stimulating Hormone (FSH), prolactin, and progesterone and found progesterone levels in the plasma were basal until the first ovulation, thereafter the pattern of progesterone secretion was typical of that documented during the breeding season. The first ovulation was found to be associated with a substantial surge of LH, a phenomena not observed during the anestrous period. Plasma FSH levels fluctuated randomly throughout anestrus and the transition into the breeding season, no pattern was able to be observed. While prolactin showed relatively high levels during the anestrous period it consistently fell to lower levels before the time of ovulation, this event was observed in normally cycling ewes and those with a photoperiod manipulated estrous/anestrous season (Walton et al., 1977).

Yuthasastrakasol et al. (1975) assayed LH, progesterone, and estradiol-17β throughout anestrus and the transition into breeding activity. Progesterone levels were basal until 25 days before the first estrus of the breeding season at which time there was a minor peak. Basal progesterone levels were also shown from 21 to 12 days before the first estrus of the breeding season. There was a major increase in progesterone beginning approximately 12 days before the first estrus of the breeding season. Other researchers have also reported luteal activity to some extent or another preceeding the first behavioral estrus of the breeding season (Goat--Kakusya, 1979, Ewe--Walton et al., 1977; Wheeler et al., 1977, Ewe lambs upon reaching puberty--Foster et al., 1975; Simaraks, 1978). It is quite possible that these increased progesterone levels were manifestations of the well documented ovulation without estrus which occurs commonly in sheep and goats. LH levels were found by Yuthasastrakasol and coworkers to fluctuate at low levels (mean of 2.3 $\pm$ 0.9 ng/ml) throughout the seasonal anestrous period with one exception, three of the four ewes sampled exhibited peaks of 20.0, 41.2, and 137.5 ng/ml, 24 days before the first behavioral estrus of the breeding season, again possibly reflecting an ovulation without estrus. Random variations in the concentrations of estrogens, deviating from a mean level of 4.4 $\pm$ 0.1 pg/ml were observed during the anestrous period. During the interval between the first and second estrus the mean estrogen level was 5.2 $\pm$ 0.3 pg/ml. A well defined peak averaging 13.3 $\pm$ 0.7 pg/ml was observed in all ewes on the day of the second estrus.

Roche et al., (1970) reported plasma LH levels in the ewe during the seasonal anestrous period of 0.25 ± 0.059 ng/ml in May, levels too low to be detected in June and July and 1.2 ± 0.397 ng/ml in August.

In 1977, Scaramuzzi and Baird, collecting serum samples from six anestrous ewes every ten minutes for four hours reported LH and estradiol-17β levels. The basal concentration of LH was 0.45 ± 0.06 ng/ml with pulses of LH (Peak values of 6.0 ± 0.3 ng/ml) occurring with an average of one pulse every five hours. A very close cause-effect type of relationship was noted between LH and estradiol-17β, with each pulse of LH being closely followed by a rise in the peripheral plasma levels of estradiol-17β.

Rawlings et al. (1977) studied the changes in the concentrations of several circulating hormones in the ewe during the late breeding season, transition into seasonal anestrus, and the early seasonal anestrous period. These researchers reported the last six cycles before the onset of seasonal anestrus were normal, except a shortened period of behavioral estrus (≤8 hours which was observed in four of the six ewes during the last pre-anestrous heat period). No change was noted in basal plasma LH levels (≤1.2 ng/ml) or LH surge values ($P < 0.05$) over the last six cycles before the onset of anestrus, except in three ewes which did not appear to exhibit an LH surge during the last behavioral estrus of the breeding season. Progesterone levels indicative of luteal development were present in the last six estrous cycles of the breeding season, even in the ewes exhibiting a shortened estrous period and no apparent preovulatory LH surge. At the last period of behavioral estrus a normal rise in estradiol-17β was followed

by a subnormal rise in serum LH (<1.2 ng/ml). Subsequently, plasma concentrations of LH, estradiol-17β, and progesterone remained at basal levels typical of the seasonal anestrous period.

The postpartum period

While much research has been conducted on the endocrinology of the postpartum period in cattle, relatively little information is available on ovine or caprine hormone profiles postpartum. Care must be taken when interpreting postpartum hormone profiles not to confound the effects of the postpartum period with those of seasonal anestrus or suckling effects. Plasma prolactin levels in nursing and dry doe goats differ significantly since suckling has been shown by a neural stimulus to reflexively release prolactin (Johke, 1970). It is postulated by Grandison et al. (1971) that prolactin depresses cyclic gonadotropin behavior at the level of the hypothalamus.

Progesterone levels in the doe during the first 3 to 4 days postpartum were measured by Kakusya (1979). These data show progesterone levels at the time of parturition to be rapidly falling and in the range of approximately 2.0 to 4.0 ng/ml. By one day postpartum, progesterone levels were 1.0 ng/ml or less where they stayed for the duration of the sampling (3-4 days). Foster and Crighton (1973a) measured plasma LH levels in the postpartum ewe induced to lamb, by photoperiod manipulation, in the breeding season. Two of the three ewes tested postpartum were suckling lambs while the other ewe was not lactating. Both lactating and the dry ewe showed levels of LH throughout the sampling period, similar to the basal values recorded for open cyclic ewes being sampled concurrently. Although the dry ewe

did exhibit an LH peak of 69.0 ng/ml on day 17 postpartum, none of the ewes showed estrus until day 54 postpartum. Laparotomies performed on day 34 postpartum revealed no corpora lutea, corpora albicantia, or even large follicles. Foote (1971) reported ovaries almost entirely devoid of follicles 2 mm or larger to day 10 postpartum.

Kann et al. (1977) reported basal plasma LH levels with small fluctuations (0.3 ng/ml - 2.0 ng/ml) during the postpartum period until the time of estrus in lactating ewes lambing in the breeding season. In another study, Wright et al. (1981), using postpartum lactating ewes lambing in the breeding season, so the postpartum endocrine events would not be confounded by seasonal anestrus endocrine events, reported low pulsatile levels of plasma LH (LH pulse amplitude--6.0 $\pm$ 0.97 ng/ml, pulse frequency--1.8 $\pm$ 0.42 pulses/6 hours). These levels were higher than those observed in cyclic diestrous ewes but still were much less than LH levels associated with preovulatory follicular development when plasma LH levels of 2.0-8.6 ng/ml and pulse frequencies of greater than one pulse per hour were detected (Baird, 1978). Prolactin levels are high in lactating ewes (300-400 ng/ml) until 50-60 days postpartum when they progressively become comparable to levels in cyclic ewes in luteal phase (50.0 ng/ml) (Kann et al., 1977). Arije et al. (1974) reported hormone levels in postparturient lactating cattle. Postpartum LH levels fluctuated between 1.0 and 3.0 ng/ml until the first LH surge which occurred an average of 98 days postpartum. Progesterone levels were less than 2.0 ng/ml throughout the postpartum anestrous period, excepting a slight rise 2-4 days before the first LH surge. Estrogens fell to 500 pg/ml at parturition and decreased to about 200 pg/ml by

five days postpartum, fluctuating at this level until two days before estrus (day 96 postpartum) when a peak of 500 pg/ml was recorded.

Generally, the postpartum period is characterized as a hormonally refractory period with basal levels of LH, progesterone, and estrogen and elevated prolactin levels. McNeilly (1980) reviewed the relationships between prolactin and gonadotropin secretion concluding that the close inverse relationship between the gonadotropins and prolactin which upon casual observation would seem to indicate a cause-effect interaction may actually be manifestations of higher neuroendocrine control.

Proposed Endocrine Mechanisms Responsible for Seasonal Anestrus

Many of the major endocrine events responsible for seasonal anestrus have been reported in the literature using the ewe as the animal model. Preliminary research (Kakusya, 1979) conducted on the goat would seem to indicate that the seasonal anestrous period in both the goat and sheep are controlled through similar endocrine mechanisms.

The estrous cycle may be explained as a cascade of hormonal events each of which must occur to initiate the next step. Interruption of any one step would terminate the cycle whereas the restoration of that step would complete the circuit and reinitiate the cycle. It is incorrect to assume that the seasonal anestrous period is a time when the reproductive system is totally inactive since many of the endocrine events of the estrous cycle remain functional in the seasonally anestrous ewe, ovarian follicles develop, produce steroids, are capable of responding to gonadotropins and can ovulate if presented with

sufficient gonadotropic stimulus (Cole and Miller, 1935; Scaramuzzi and Baird, 1977). Gonadotropins are secreted, tonic LH continues to be secreted in pulsatile fashion (but at reduced frequency compared to the breeding season), and ovarian steroids demonstrate both positive and negative feedback effects on gonadotropins (Goding et al., 1969; Karsch and Foster, 1975; Roche et al., 1970; Scaramuzzi and Baird, 1977). However, the LH surge and ovulation do not occur during anestrus.

Several theories have been advanced to explain the endocrine basis of seasonal anestrus. These hypotheses were reviewed by Karsch and Foster (1981) and include the following:

1. An impaired follicular development or response to LH due to inadequate secretion of FSH (Legan and Karsch, 1979)
2. Decreased response of the LH surge system to the positive feedback effects of estradiol (Land et al., 1977; Legan and Karsch, 1979)
3. Increased prolactin levels (Walton et al., 1977; McNeilly, 1980)
4. A seasonal variation in the sensitivity of the hypothalamic LH tonic center to the negative feedback effects of estradiol (Legan et al., 1977)

As to the first hypothesis, follicles developed during the anestrous season are fully able to respond to gonadotropins and secrete large quantities of steroidal hormones (Scaramuzzi and Baird, 1977: Yuthasastrakasol et al., 1975). FSH levels during anestrous are comparable to basal levels during the breeding season (Walton et al., 1977). But as of this date no one has reported the response of the follicle to gonadotropins throughout the year so we cannot rule this

theory out as a viable endocrine change which may assist in explaining the endocrine changes responsible for seasonal anestrus.

Land et al. (1977) reported a decrease in the sensitivity of the LH surge center to the positive feedback of estradiol. But more recent research suggests that a sustained (48-60 hours) preovulatory rise of 2 to 10 pg/ml of estradiol (Physiologic levels sufficient to trigger an LH surge in the breeding season) is sufficient to trigger the LH surge during the anestrous season (Legan and Karsch, 1979; Goodman and Karsch, 1980). The weight of evidence seems to make this possible mechanism untenable.

Walton et al. (1977) proposed that increased prolactin levels may play a role in causing seasonal anestrus. High levels of prolactin have been observed in several anestrus conditions (seasonal anestrus--Walton et al., 1977; lactational anestrus--Kann et al., 1977; and certain acyclic conditions in women--Aono et al., 1976). A defect in the estradiol positive feedback mechanism has been reported in hyperprolactinemia and certain types of amenorrhoea in women (Baird et al., 1979; Aono et al., 1976; Besser et al., 1972; Glass et al., 1975). This hypothesis, however, does not seem to explain the acyclicity of seasonally anestrous ewes, despite elevated prolactin levels during this period, since as pointed out by Legan and Karsch in 1979, there is not decrease in the sensitivity of the estradiol positive feedback on the LH surge system during seasonal anestrus. High prolactin levels, however, may play an important role in other types of anestrus (Karsch and Foster, 1981).

With regard to the fourth possibility, investigations by Legan et al. (1977), Hauger et al. (1977), Karsch et al. (1977), Rawlings et al. (1977), and Karsch et al. (1978) have shown quite conclusively that there is a seasonal change in the centers controlling tonic gonadotropin secretion to the negative feedback of estradiol. During the anestrous season estradiol acts as a potent inhibitor of tonic LH and FSH secretion (Legan and Karsch, 1980), whereas during the breeding season estradiol was found to be a somewhat less effective inhibitor of gonadotropin release. The following generalized scheme of endocrine events would characterize the hypothesis of Legan and Karsch (1979), describing transition from the breeding season into the seasonal anestrous period. The decreasing progesterone levels, reflecting the destruction of the last corpus luteum of the breeding season, allows an increase in the pulse frequency of the gonadotropins (Goodman, 1981). These higher gonadotropin levels stimulate the ovary to an increased estrogen production. These increased estrogen levels feedback to the centers controlling gonadotropin secretion and since these centers are hypersensitive to estrogen at this time of year, estrogen acts as a potent inhibitor of tonic LH secretion and consequently estrogen levels are not maintained at threshold levels for a sufficient time to trigger the LH surge, which otherwise would have triggered ovulation. To date, this hypothesis is the most tenable to explain the anovulatory period of seasonal anestrus.

The pineal gland has recently been implicated in the mediation of photoperiodic control of seasonal breeding by changing the responsiveness of the tonic LH center to estrogen negative feedback (Bittman

et al., 1981). This proposal incorporates photoperiod, which is the major environmental factor controlling seasonally polyestrus species into the endocrine mechanism proposed by Legan and Karsch.

It has been reported that the endocrine events occurring at puberty may be similar to those responsible for transition from seasonal anestrus into breeding activity. A definite change in the effectiveness of estrogen negative feedback has been observed (Foster and Ryan, 1979; Ryan and Foster, 1980; Ojeda et al., 1980).

The anestrus condition associated with the postpartum period has also been recently characterized as a time when estrogen is a potent inhibitor of gonadotropin secretion (Wright et al., 1981).

Hormonal Changes and Ovarian Activity Following Exogenous GnRH Administration

As early as 1947, Green and Harris proposed the regulation of the anterior pituitary by a hypothalamic substance transported through the hypothalamo - hypophyseal portal system. Schally et al. (1971) first isolated this gonadotropin releasing factor, and in that same year Matsua et al. determined the amino acid sequence. GnRH was found to be a decapetide functioning to control the release of gonadotropin from the pituitary. Eskay et al. (1977) have shown GnRH to be secreted by the hypothalamus in a pulsatile manner, this pulsatile GnRH secretion being expressed in the well documented pulsatile LH secretion pattern. The response of the anterior pituitary to GnRH has been shown to be affected by the level of circulating estrogens, with an increase in circulating levels of estrogen being characteristic of an increased sensitivity to

GnRH during the breeding season. During the anestrous season and period of transition into or out of the breeding season, estradiol has been reported to reduce the sensitivity of the anterior pituitary to GnRH (Moss and Nett, 1980; Reeves et al., 1971). The literature contains only one report of the response to GnRH in the goat. van der Westhuysen (1978) reported the estrus response and changes in plasma progesterone following GnRH in 2 goat breeds (Angora and Boer goat), but upon injection of GnRH a male goat was suddenly introduced, therefore, the response to GnRH was likely to have been confounded by introduction of the male which has been shown to induce and syncronize ovulation in female goats and sheep (Skinner and Hofmeyr, 1969; Shelton, 1960). In 1974, Symons et al. studied the gonadotropic response of anestrous and cyclic ewes to GnRH. A single, subcutaneous (s.c.), injection of 100 μg GnRH in anestrous ewes resulted in a peak of approximately 75 ng/ml LH (mean of three animals). Two anestrous ewes were given intravenous (i.v.) injections of 100 μg GnRH at 0 and 3 hours. There was considerable difference between animals in the LH responses to this injection schedule, one animal showing a peak of 38 ng/ml and the other 150 ng/ml. These two peaks were observed approximately 2.5 hours following the initial injection. The second injection 3 hours later was found to give a much more rapid and heightened response. Twenty to thirty minutes after the second injection LH levels peaked at 121 and 186 ng/ml. The first injection seemed to sensitize the anterior pituitary to the second injection 3 hours later. In contrast, Symons and coworkers reported a profound decrease in LH response to GnRH if the interval between injections was 24 hours. In

this study, subcutaneous injections seemed to give peak plasma gonadotropin levels approximately 30 mintues later than intravenous injections, and over the range studied, 100-500 ug there was an indication of a dose-dependent relationship. Jenkin and coworkers (1977) reported the pituitary responsiveness to 200 ug synthetic GnRH at various reproductive stages in the ewe. The time from GnRH injection to peak plasma LH did not differ significantly in any of the several reproductive phases examined (mean ± SEM = 100 ± 2 mintues). Both peak LH concentrations and the area under the curve of LH were measured and were highly correlated (r = 0.96). Table 1 reports these data below.

Table 1. Mean LH response to injection of 200 ug GnRH (Jenkin et al., 1977)

Reproductive state	Time of injection	No. of animals	Maximum LH concentration (ng/ml) following 200 ug GnRH (i.v.)
Seasonal anestrus	April-August	11	63.2 ± 7.7
Cyclic	Days 5-13 of estrous cycle	15	63.8 ± 12.0
Postpartum (lactating)	1-2 weeks	7	29.6 ± 7.5
	3-5 weeks	7	30.6 ± 5.2
	5-7 weeks	6	38.4 ± 9.4
	8-10 weeks	6	60.3 ± 18.3
Postpartum (not lactating)	1-2 weeks	3	30.2 ± 10.3
	3-5 weeks	6	76.8 ± 21.2
	5-7 weeks	7	53.7 ± 4.2
	8-10 weeks	7	61.1 ± 14.1

Foster and Crighton (1973b) reported that cyclic ewes injected with 150 ug GnRH (i.v.) responded with peak LH levels of 65-75 ng/ml, 90-120 minutes after injection. LH levels had returned to baseline by

180 minutes. Ovulation was observed in both ewes via laparoscopy two days post-GnRH treatment. Foster and Crighton reported two cyclic ewes treated with 50 µg GnRH (i.v.) failed to ovulate. Anestrous ewes injected with 150 µg GnRH (i.v.) responded with mean LH peak values of 110 ng/ml and ovulation was observed in the majority of animals. Wright et al. (1980) reported the pituitary responsiveness to GnRH in Merino ewes postpartum (Lambing in the breeding season). On day 14 postpartum, a challenge of 50 µg GnRH (i.v.) yielded a mean LH peak level of 37.8 ± 3.2 (SEM) ng/ml, n=51. Fernandes et al. (1978) reported the LH release in response to GnRH during the postpartum period of dairy cows. The results indicate that LH release was not fully restored until ten days postpartum. Kesler et al. (1977) studying pituitary response to GnRH in the cow reported similar results.

Pituitary LH Levels During Several Reproductive Phases

Pituitary LH levels have been reported by several investigators. Pretorius (1974) using bioassay techniques, slaughtered six Angora goats on each of the following days of a normal estrous cycle: proestrus (day -1), early estrus (day 0), late estrus (day 1), early luteal phase (day 6), and mid-luteal phase (day 18). Actual pituitary LH values were not given by Pretorius, trends were only reported. LH activity increased gradually from day 1 reaching a high on day 18. The pituitary LH levels then dropped sharply and continued to decrease through estrus reaching a low level during late estrus. The increase in LH levels was more rapid in the first and last third of the cycle than between day 6-12. Pituitary LH levels during the anestrous period were comparable

to those of the mid-luteal phase of the breeding season and were maintained at this relatively constant level throughout anestrus. Pituitary LH concentrations at different reproductive stages of the sheep were reported by Jenkin et al. (1977), and listed in tabular form below.

Table 2. Mean pituitary LH levels during several reproductive phases (Jenkin et al., 1977).

Reproductive state	Time of collection	No. of animals	Mean pituitary LH concentration ± SEM (μg/g tissue)
Anestrus	April - August	7	1135.0 ± 302.3
Cyclic	Days 5-13 of estrous cycle	5	1354.5 ± 207.5
Postpartum (lactating)	1-2 weeks	4	511.5 ± 145.4
	3-5 weeks	4	819.2 ± 117.1
	5-7 weeks	4	1127.0 ± 217.7
	8-10 weeks	3	846.1 ± 89.4
Postpartum (not lactating)	3-5 weeks	4	1082.8 ± 57.5
	5-7 weeks	4	995.0 ± 45.8
	8-10 weeks	4	1041.0 ± 199.7

Roche et al. (1970) reported pituitary LH levels in estrous and anestrous ewes. These researchers reported a mean concentration of LH in pituitaries of 112 ± 15 (μg/g tissue ± SEM) on day 1 of the estrous cycle, increasing steadily to 374 ± 47 on day 9, concentrations then fluctuated between 613 ± 67 and 537 ± 32 on days 11-15, and increased to 998 ± 91 during the proestrus. In addition, six ewes were slaughtered during each month of the anestrous season (May - August). The pituitary LH concentration fluctuated between 431 ± 27 and 300 ± 42 (μg/g tissue ± SEM) during this period. No statistical differences in LH content were observed during the seasonal anestrous period.

Chamley et al. (1976) reported pituitary LH levels in the anestrous season. Ten ewes were slaughtered and pituitary LH content was measured using RIA techniques. Pituitary LH content of non-pregnant anestrous ewes were an average of 893.8 ± 201.3 μg. Chakraborty et al. (1974) found pituitary LH levels in anestrous ewes to be 214.9 ± 68.6 (μg/pituitary ± SEM) with a mean pituitary dry weight of 352.5 ± 28.4 (SEM) mg or 0.65 ± 0.2 (SEM) μg LH/mg pituitary. LH concentrations in the pituitaries of postpartum ewes were reported by Foote (1971). LH levels reported during this period were very low, showing a trend (nonsignificant) for pituitary LH concentration to increase from day 0 to 24 postpartum in lactating ewes. Concentrations of 0.087, 0.111, 0.237, 0.354, and 0.427 μg/mg on days 0, 3, 10, 17, and 24, respectively, were observed. Pituitary LH concentrations tended to be higher in the nonlactating ewe than in the lactating ewe on day 24 (1.028 vs. 0.427 μg/mg, $P < 0.05$).

MATERIALS AND METHODS

Forty Spanish and Spanish-dairy (Nubian and Saanen) cross goats from 18-42 months of age were used in this research conducted from November 1981 to June 1982. The experimental animals were fed alfalfa hay pellets at the level required to meet their nutritional requirements according to NRC recommendations. In addition, each animal was provided clean water, ad libitum, housing, and outside pen space and otherwise managed to assure standardized and humane treatment and minimum stress.

Each animal was weighed at the beginning and the end of the experimental period.

The experimental design is outlined in Tables 3 and 4. Details of the experimental method not provided within these tables are described in the "Procedures used to Measure Parameters" section.

Procedures Used to Measure Parameters

Estrus determination

Estrus was determined by the use of a vasectomized buck with a painted brisket. The buck was run continuously with the does and checks for estrus were made at approximately 12 hour intervals, mornings and evenings, from mid-October until April. Estrus checks were made at four hour intervals where more precise measures were required for blood collection.

Table 3. Experimental design, Experiment I

Parameter	Reproductive Phase		
	Estrous Cycle (Breeding Season)	Seasonal Anestrus	Early Postpartum Period
Number of does	10	10	9
Hormone profile a. progesterone	Serum samples daily during the estrous cycle.	Serum samples daily during a 21 day period beginning approximately two cycle lengths following the last estrus of the breeding season.	Serum samples daily for a 14-17 day period beginning on the day of parturition.
b. LH	Serum samples at four hour intervals for 48 hours beginning immediately after the detection of estrus.	Serum samples at four hour intervals for 48 hours beginning at the initiation of the progesterone sampling period.	Serum samples at four hour intervals for 48 hours beginning within 6 hours of parturition
Ovarian Response	Record the number of corpora lutea and follicles ≥6 mm between day 7 and 11 of the estrous cycle	Record the number of corpora lutea and follicles ≥6 mm between day 7 and 11 of the progesterone sampling period.	Record the number of corpora lutea and follicles ≥6 mm between day 7 and 11 postpartum.

Table 4. Experimental design, Experiment II

Parameter	Reproductive Phase		
	Estrous Cycle (Breeding Season)	Seasonal Anestrus	Early Postpartum Period
Number of does	5	4	5
Anterior pituitary LH levels	Anterior pituitary removal on days 15-17 of the estrous cycle.	Anterior pituitary removal on days 15-17 of the progesterone sampling period of Experiment I.	Anterior pituitary removal on days 15-17 postpartum.
Number of does	5	5	5
Plasma LH levels following GnRH administration	Administration of GnRH on days 15-17 of the estrous cycle. Serum samples previous to GnRH treatment and after GnRH at 1/4, 1/2, and 4 hour intervals until 24 hours post GnRH administration.	Administration of GnRH on day 30 of the progesterone sampling period of Experiment I. Serum samples previous to GnRH treatment and after GnRH at 1/4, 1/2, and 4 hour intervals until 24 hours post GnRH administration.	Administration of GnRH on days 15-17 postpartum. Serum samples previous to GnRH treatment and after GnRH at 1/4, 1/2, and 4 hour intervals until 24 hours post GnRH adminstration.
Ovulation following GnRH administration	Record the number of corpora lutea and follicles ≥6 mm on day 9 post GnRH administration.	Recorded the number of corpora lutea and follicles ≥6 mm on day 9 post GnRH administration.	Record the number of corpora lutea and follicles ≥6 mm on day 9 post GnRH administration.

Fertile mating

Twelve does were randomly designated for the postpartum group. All does were implanted subcutaneously with progesterone containing silicone rubber implants, following the procedures reported by Vaught in 1976, for 17 days to syncronize their estrous cycles. Two bucks of Spanish-Saanen and Spanish-Nubian breeding, shown to be fertile by a physical examination and semen evaluation, conducted on the same day the bucks were exposed to the does, were used for breeding. Immediately upon removal of the implants, the females involved in this group were continuously penned with the above mentioned fertile bucks for approximately 60 days.

Blood collection

A. In Experiment I, blood samples were collected during each of the three reproductive phases outlined previously for progesterone and LH analysis. During the estrous cycle, blood collections were initiated as soon as the doe exhibited estrus. Initiation of bleeding of the seasonal anestrus group began approximately two cycle lengths following the last observed estrus activity of the breeding season. Blood collection began within six hours after parturition in all postpartum does.

Blood samples were collected every four hours for 48 hours to characterize the LH surge and thereafter daily, at 8 a.m., for the duration of the estrous cycle, progesterone sampling period in the seasonal anestrus group, and during the first 14-17 days postpartum, to establish progesterone profiles in the three reproductive phases, respectively.

A volume of ten ml of blood were taken via jugular venipuncture at all bleedings and allowed to clot overnight at 4° C. Serum was removed by centrifugation, frozen and stored at -20° C until analyzed.

B. Blood samples were also taken in Experiment II for LH analysis. Serum sampling was initiated 15 minutes before, then immediately preceeding the initial GnRH injection. After the initial GnRH injection, serum samples were collected every 15 minutes for six hours, every 30 minutes for the next two hours, and thereafter every four hours until 24 hours after the initial GnRH injection. This schedule was followed closely in each of the three reproductive phases. A volume of five ml of blood were collected via jugular venipuncture at all bleedings and allowed to clot overnight at 4° C. The serum was again removed by centrifugation, frozen, and stored at -20° C until analyzed.

GnRH administration

GnRH[1] was injected subcutaneously in two doses of 100 µg diluted in one ml of physiologic saline and administered three hours apart on days 15-17 of the estrous cycle and progesterone sampling period in the seasonal anestrus group, and on day 16 postpartum in the postpartum group. Symons et al. (1974) reported that administration of 100 µg GnRH resulted in a significant LH response of the approximate magnitude of the preovulatory LH surge, furthermore, the first injection sensitized the pituitary to GnRH when the interval between the two injections was

[1]GnRH was generously supplied by Parke Davis Co., Detroit, Michigan.

three hours. This injection schedule and dosage was therefore selected for two reasons: (1) It provided a significant LH response which could be readily compared to the results obtained from experiments using the ewe as the animal model, and (2) As far as possible, considering the fact that we administered injections rather than infused GnRH, this schedule maximized the pituitary LH release to 200 μg GnRH.

Anterior pituitary removal

Immediately upon sacrificing the doe the anterior pituitary was removed from the sella turcica and placed on ice. All extraneous tissue (including the posterior lobe) was trimmed away, the pituitary weighed, and stored at -20° C until assayed.

Ovarian activity

In Experiment I, the ovaries were observed, via laparoscopy, between day 7 and 11 of the estrous cycle, the assigned progesterone sampling period during seasonal anestrus, and the early postpartum period. The number of corpora lutea and follicles ≥6 mm were recorded. In Experiment II, the ovaries were observed, via laparoscopy, nine days following GnRH injections in each of the three reproductive stages. The number of corpora lutea and follicles ≥6 mm were recorded.

Laparoscopic observations

Laparoscopy was accomplished using the general techniques described by Seeger and Klatt (1980) with some modifications as considered necessary. An 8 mm Eder laparoscope with an OL 150,

Eder light source were employed. Food and water were withheld from all animals for at least 24 hours prior to laparoscopic observations. Animals were sedated with 10 mg Rompun (Xylazine), injected intramuscularly prior to all observations. The sedated does were restrained on a laparotomy cradle (Hulet and Foote, 1968), in a head down dorsal recumbent position with the cradle sloped at an approximate 45^{o} angle. An area of the abdomen 15 to 20 cm cranial to the mammary glands and extending approximately 10 cm to each side of the midline was clipped and disinfected with soap, water, and phenylmercuric nitrate solution. A sterile field was not maintained during observations since a very low post-operative infection rate had been observed in previous investigations using the laparoscope (Seeger and Klatt, 1980), but a conscientious effort was made to keep the immediate surgical site, the laparoscopic instruments, and the operator's hands as uncontaminated as possible. Two small skin incisions approximately one inch in length were made approximately three inches cranial to the mammary gland and one to two inches lateral to the midline, and the larger and smaller trocar-cannula (sleeve) apparatus were inserted through the body wall. A blunt manipulating rod was used in the smaller cannula to manipulate the reproductive tract during observations. After observations were completed, the skin incisions were closed with skin clips, and each animal was given 600,000 units penicillin G, procaine, and dihydrostreptomycin as a preventive measure to discourage post-operative infections.

Hormone analysis

All hormone assays were performed at the International Sheep and Goat Institute Physiology Laboratory, Utah State University, by a laboratory technician.

LH--Serum LH concentrations were measured using the double antibody method of radioimmunoassay (RIA), described by Niswender et al. (1969). The standard curve was prepared in duplicate using nine doses of purified ovine LH standard (NIH-LH-S15)[2] ranging from 0.1 to 40.0 ng. Unknown serum samples were assayed in duplicate using 200 µl of serum per assay tube. The purified LH standard (LER-1056-C2)[3] was radioiodinated with ^{125}I according to established procedures.

Pituitary LH analysis--Anterior pituitary glands were homogenized in 15 ml cold PBS, centrifuged at 15,000 x g for 30 minutes and the supernatants diluted 1:2000 for LH assay (Admundson and Wheaton, 1979), using the same procedures as described above for serum LH analysis.

Progesterone analysis--Progesterone analysis was by Radioimmunoassay following the general procedure described by Ford et al. (1979). The summary of procedures with included modifications are as follows:

Progesterone was extracted from 0.2 ml. of plasma twice with 2 ml of a 1:2 benzene:hexane mixture. Glass distilled pesticide grade benzene and hexane were mixed well, and allowed to equilibrate

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[2]Purified ovine LH standard was obtained from the National Institute of Health, Bethesda, Maryland.

[3]Purified standard supplied by Dr. Leo Reichert, Albany Medical College, Albany, New York.

at room temperature for 30 minutes before extractions. After mixing each tube for 30 seconds, the tubes were centrifuged at 1000 x g for 10 minutes. The aqueous phase was frozen in an ethanol-dry ice bath and the solvent from both extractions were combined and evaporated under filtered air in a 37^{o} C water bath.

In each assay, four pooled plasma and two water blanks were also extracted and assayed. Percent recovery of progesterone from plasma was estimated for each assay by the addition of a known amount of ^{3}H-Progesterone to pooled plasma, which was extracted and collected in scintillation vials for counting. Recovery rate ranged from 97.5 - 99.0 percent. A standard curve was run with each set of unknown samples.

Statistical methods

Ovarian activity data was analyzed using either chi-square analysis for the binomial data (number of does ovulating and number of does having follicles $\geq$6 mm), or analysis of variance, with a square root transformation to meet the assumption of homogeneity of variance (Steel and Torrie, 1980).

Mean basal progesterone and tonic LH levels within treatment groups were found by computing the mean LH or progesterone level during the respective sampling period for each individual animal. Thereafter, values obtained for animals within treatment groups were used to calculate a mean and standard error. Basal LH and progesterone levels were compared using the one way analysis of variance. When

treatment effects were significant, differences between means were determined by the Least Significant Difference (LSD) test (Steel and Torrie, 1980).

The responsiveness of the pituitary to GnRH was assessed by comparing the area under the curve of LH release from the time of the first GnRH injection until eight hours following the first GnRH injection in all three treatment groups. The area under the curve was calculated, by the trapezoidal rule (Abramowitz and Stegun, 1968). The time period over which the LH response was measure was selected on the basis that LH levels had approximately returned to preinjection levels by eight hours following the first injection of GnRH so that the area under the curve expressed in ng/hr x ml, was proproportional to the total amount of LH released. These data were subjected to one way analysis of variance and the LSD multiple means comparison test.

RESULTS

Estrous Cycle Length

Estrous cycle lengths were measured during the fall and winter of 1981-82. A total of 40 goats were observed to record data on 107 estrous cycles. The overall mean cycle length was 20.22 ± 0.36 days (range of 7.5 to 41.5 days). These cycle lengths fell easily into three categories: short cycles, intermediate cycles, and long cycles. One short cycle of 7.5 days was recorded. Three animals exhibited long cycles, having a mean cycle length of 39.83 ± 1.01 days. All of the other 103 observations fell within a range of 18.0 - 24.5 days having a mean cycle length of 19.78 ± 0.12 days. Estrous activity continued in the majority of does until approximately the first two weeks of March, 1982, with the last observed behavioral estrus occurring on April 12, 1982.

There were indications that introduction of the buck into the does' pen resulted in syncronization of the does' estrous cycles, a phenomena reported by other researchers (Skinner and Hofmeyr, 1969; Shelton, 1960). However, control data were not recorded, therefore, conclusions may not be made. The buck was introduced into the does' pen on October 9, 1981 (previous to this study the does had not been exposed to a buck for an extended period of time), and estrous data was observed starting on October 16, 1981. Between November 3 and November 7, 1981, 90.5 percent (38 of 42) of the does exhibited estrus,

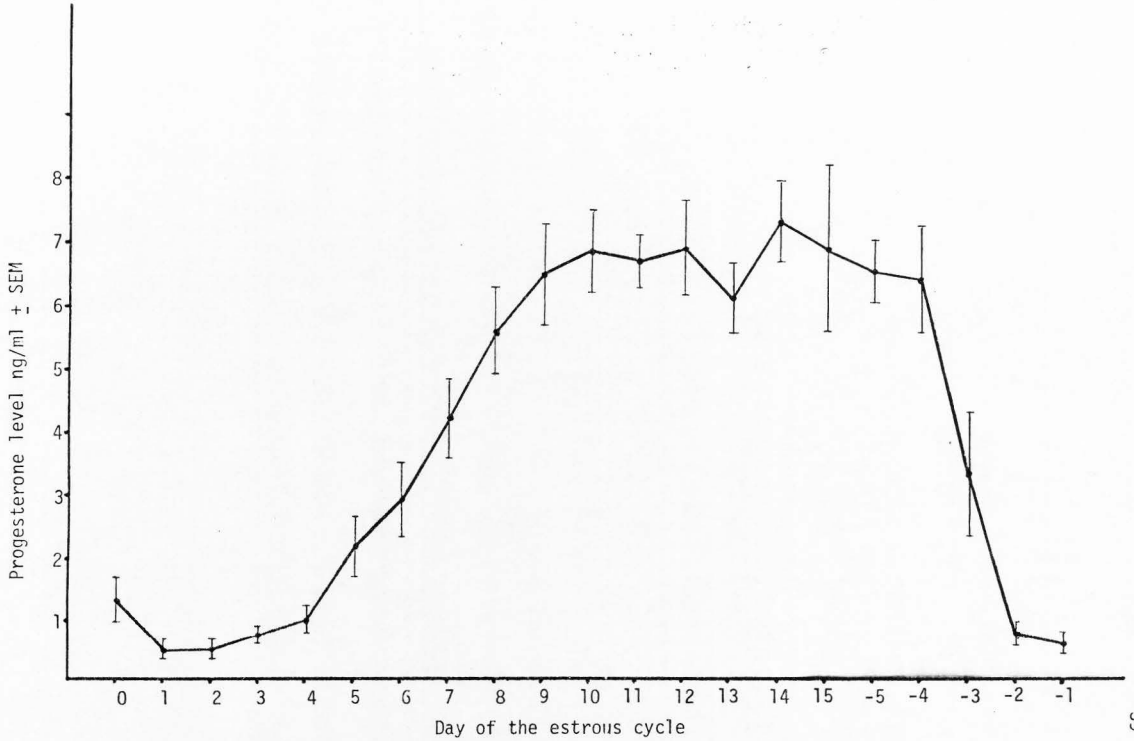
with 64.3 percent of the animals showing signs of behavioral estrus in the two day period of November 4-6, 1981.

Progesterone Levels During Three Reproductive Phases (Breeding Season, Seasonal Anestrus, and the Early Postpartum Period)

Progesterone levels in the peripheral plasma of the goat followed the same general pattern as previously reported (Romm, 1979; Kakusya, 1979; Jones and Knifton, 1972; Thornburn and Schnieder, 1971). The mean serum progesterone levels for ten does during the estrous cycle are shown in Figure 1 and listed in tabular form in Table 5. Due to variation in cycle lengths, the last five days of the cycle are related to the upcoming estrous period, and designated as -5, -4, -3, -2, and -1.

The mean serum progesterone level during the estrous cycle was 4.01 $\pm$ 0.23 ng/ml. Progesterone levels were low (<1.5 ng/ml) at the time of estrus (day 0) and for an additional 3-4 days. On day 3-4 of the cycle, progesterone levels began to increase, reaching a level of 6.48 $\pm$ 0.78 ng/ml on day 9. Fluctuations between 6.12 $\pm$ 0.55 and 7.31 $\pm$ 0.6 ng/ml were observed from day 9 to -4 at which time a sharp drop in progesterone levels occurred in 7 of the 10 animals. A similar precipitous drop occurred in the other three does on day -3 with all does reaching low levels (<2 ng/ml) by day -1.

Progesterone levels in 10 seasonally anestrous does are reported in Figure 2 and Table 6. The overall mean level was basal, 0.65 $\pm$ 0.03 ng/ml with a range of 0.03 - 1.64 ng/ml.


Progesterone level ng/ml ± SEM
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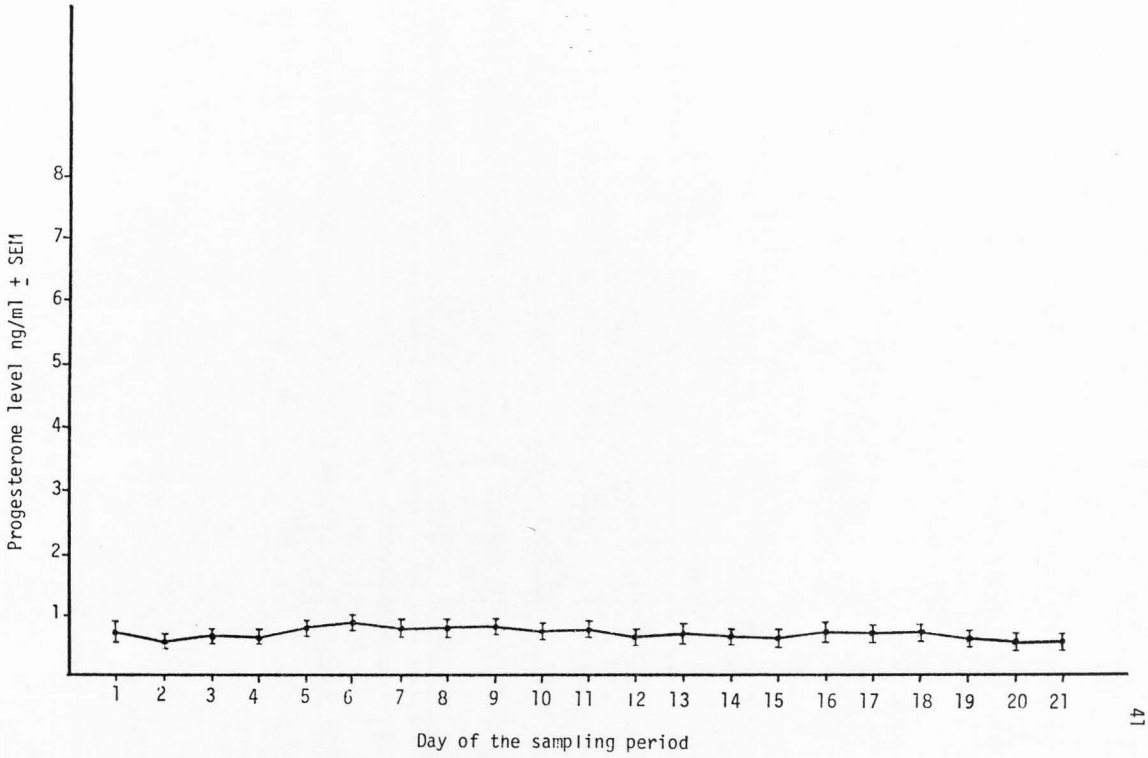
5
4
3
2
1
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 -5 -4 -3 -2 -1
Day of the estrous cycle

Table 5. Mean caprine serum progesterone levels during one estrous cycle of the breeding season (November 23, 1981 - December 14, 1981), n=11. -Day 0 = day of estrus.

Day of the estrous cycle	Progesterone level ng/ml ± SEM	Range ng/ml
0	1.31 ± 0.37	0.51 - 2.10
1	0.45 ± 0.14	0.03 - 1.41
2	0.47 ± 0.12	0.02 - 1.20
3	0.72 ± 0.17	0.08 - 1.62
4	1.01 ± 0.23	0.19 - 2.23
5	2.19 ± 0.48	0.50 - 5.33
6	2.91 ± 0.61	0.71 - 6.28
7	4.20 ± 0.58	1.07 - 6.83
8	5.57 ± 0.67	3.22 - 9.13
9	6.48 ± 0.78	3.55 - 10.20
10	6.86 ± 0.63	4.19 - 10.29
11	6.71 ± 0.43	5.37 - 9.79
12	6.89 ± 0.75	3.07 - 10.69
13	6.12 ± 0.55	3.20 - 9.80
14	7.31 ± 0.60	3.68 - 10.59
15	6.88 ± 1.35	2.68 - 10.22
-5	6.52 ± 0.51	3.10 - 8.39
-4	6.37 ± 0.85	1.77 - 10.79
-3	3.32 ± 1.02	0.47 - 10.96
-2	0.71 ± 0.20	0.12 - 2.08
-1	0.54 ± 0.17	0.11 - 1.64


Progesterone level ng/ml ± SEM
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7
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1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Day of the sampling period

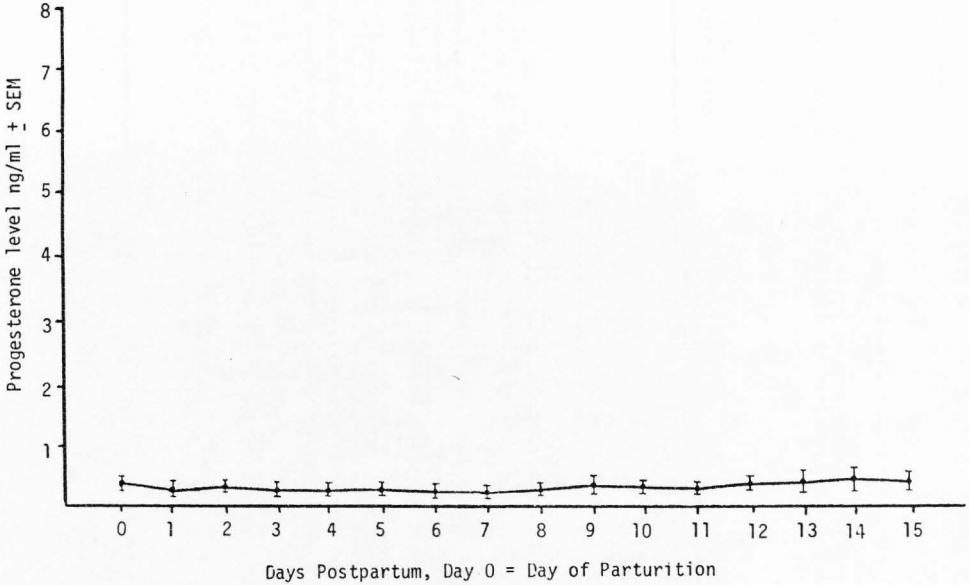
Table 6. Mean caprine serum progesterone levels on 21 consecutive days during the seasonal anestrous period (May 10-30, 1982), n=10.

Day of the sampling period	Progesterone level ng/ml ± SEM	Range ng/ml
1	0.69 ± 0.19	0.05 - 1.64
2	0.54 ± 0.14	0.10 - 1.34
3	0.61 ± 0.09	0.30 - 1.02
4	0.59 ± 0.10	0.08 - 1.15
5	0.73 ± 0.12	0.05 - 1.24
6	0.83 ± 0.14	0.09 - 1.27
7	0.74 ± 0.15	0.06 - 1.32
8	0.73 ± 0.11	0.23 - 1.07
9	0.76 ± 0.14	0.27 - 1.39
10	0.67 ± 0.15	0.06 - 1.47
11	0.74 ± 0.12	0.07 - 1.37
12	0.60 ± 0.14	0.06 - 1.55
13	0.63 ± 0.14	0.18 - 1.44
14	0.62 ± 0.11	0.19 - 1.16
15	0.56 ± 0.12	0.05 - 1.16
16	0.66 ± 0.11	0.08 - 1.22
17	0.67 ± 0.11	0.20 - 1.11
18	0.70 ± 0.12	0.11 - 1.19
19	0.57 ± 0.11	0.10 - 1.06
20	0.52 ± 0.12	0.03 - 1.07
21	0.53 ± 0.10	0.04 - 1.00

Mean serum progesterone levels in the early postpartum doe are reported in Figure 3 and Table 7. The overall mean level was basal (0.30 ± 0.02 ng/ml with a range of 0.01 - 0.91 ng/ml) throughout the sixteen day sampling period. Mean serum progesterone levels during the anestrous season were significantly greater ($P < 0.01$) than those of the postpartum period (0.65 ± 0.03 vs. 0.30 ± 0.02 ng/ml).

Serum Luteinizing Hormone Levels During Three Reproductive Phases (Breeding Season, Seasonal Anestrus, and the Early Postpartum Period)

Serum LH levels during the estrous cycles of ten goats are reported in Figure 4 and Table 8. Observations were made every four hours for 48 hours and thereafter daily, beginning with the detection of behavioral estrus. At the time of estrus, mean LH levels were 5.1 ± 0.27 ng/ml, thereafter, LH levels began a rapid rise to mean LH peak levels of 187.86 ± 3.95 ng/ml, (range 167.71 - 204.7 ng/ml) which occurred an average of 13.2 ± 1.47 hours after the onset of estrus. The duration of the elevated LH levels associated with the LH surge was 9.6 ± 1.1 hours (duration of the LH surge was calculated by measuring the time period in which LH levels were elevated above an arbitrary value of 10 ng/ml, which appeared to be the point above which the preovulatory LH surge was initiated). Serum LH levels returned to low levels of 3.6 ± 2.7 ng/ml by 24 hours post estrus and remained at low levels (overall mean not including the LH surge = 1.11 ± 0.13 ng/ml) for the rest of the cycle. A slight


Progesterone level ng/ml ± SEM
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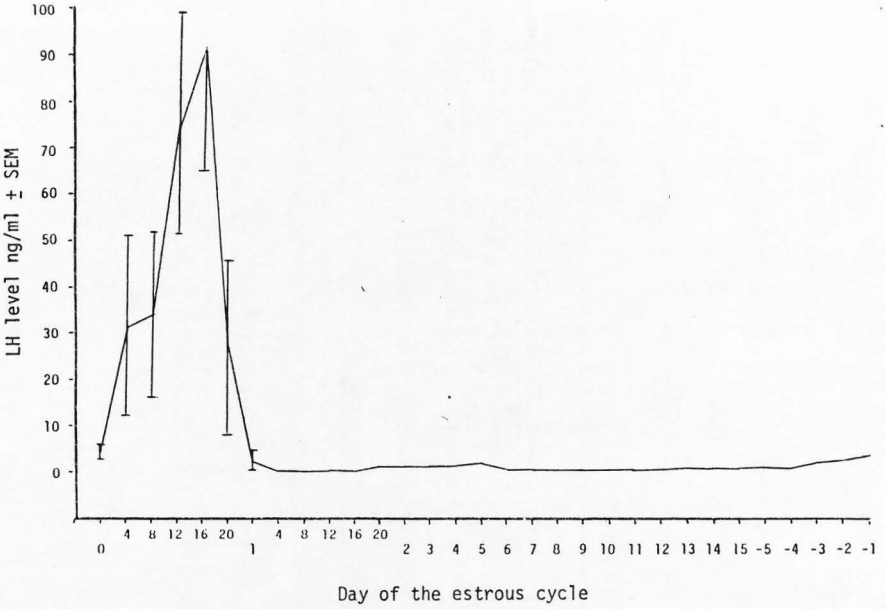
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Days Postpartum, Day 0 = Day of Parturition

Table 7. Mean caprine serum progesterone levels during the early postpartum period (sampling was initiated within six hours of parturition and thereafter daily at 8 a.m., May 19, 1982 - June 7, 1982), n=9.

Days Postpartum Day 0 = Day of Parturition	Progesterone level ng/ml ± SEM	Range ng/ml
0	0.39 ± 0.04	0.21 - 0.53
1	0.24 ± 0.04	0.03 - 0.44
2	0.24 ± 0.06	0.03 - 0.55
3	0.28 ± 0.05	0.01 - 0.55
4	0.26 ± 0.07	0.01 - 0.67
5	0.33 ± 0.08	0.08 - 0.91
6	0.26 ± 0.06	0.02 - 0.55
7	0.22 ± 0.06	0.02 - 0.46
8	0.27 ± 0.05	0.03 - 0.43
9	0.35 ± 0.07	0.01 - 0.76
10	0.32 ± 0.08	0.02 - 0.75
11	0.28 ± 0.04	0.08 - 0.43
12	0.36 ± 0.07	0.09 - 0.63
13	0.38 ± 0.12	0.09 - 0.82
14	0.49 ± 0.14	0.06 - 0.91
15	0.39 ± 0.06	0.29 - 0.51


LH level ng/ml ± SEM
100
90
80
70
60
50
40
30
20
10
0
0 4 8 12 16 20 1 4 8 12 16 20 2 3 4 5 6 7 8 9 10 11 12 13 14 15 -5 -4 -3 -2 -1
Day of the estrous cycle

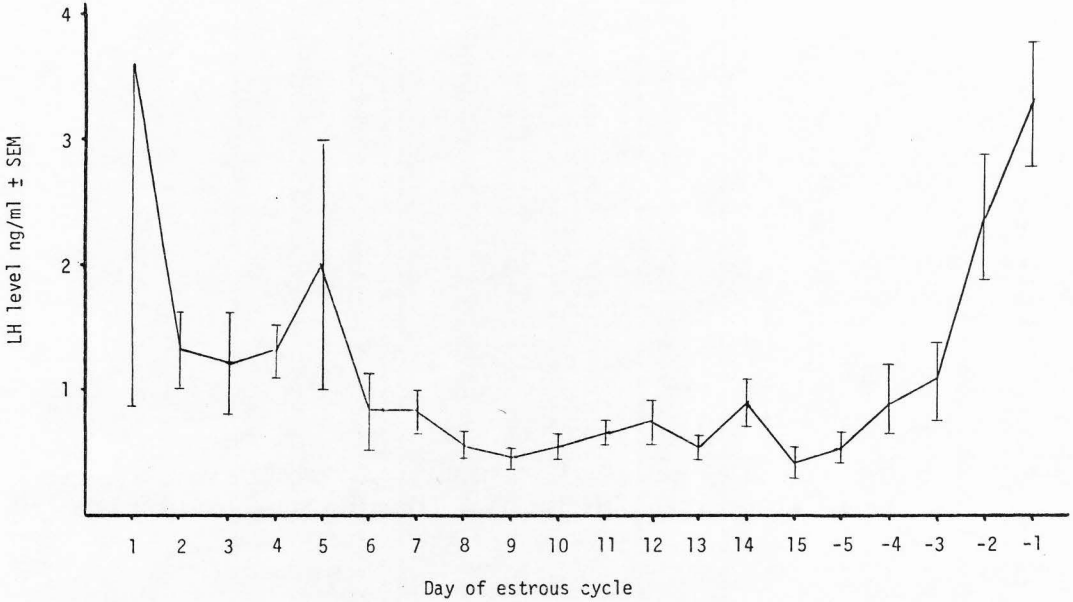

LH level ng/ml ± SEM
4
3
2
1
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 -5 -4 -3 -2 -1
Day of estrous cycle

Table 8. Mean caprine serum LH levels during one estrous cycle of the breeding season (November 23, 1981 - December 14, 1981), n=10. Day 0 = the day of estrus.

Day of the estrous cycle			
Day	Hour	LH level ng/ml ± SEM	Range ng/ml
0	0	5.1 ± 1.2	1.02 - 10.72
	4	32.7 ± 19.9	1.58 - 204.63
	8	34.5 ± 18.6	3.04 - 196.34
	12	75.1 ± 24.4	2.23 - 183.49
	16	92.7 ± 27.2	0.90 - 204.70
	20	28.7 ± 18.4	0.25 - 191.24
1	0	3.6 ± 2.7	0.15 - 27.99
	4	0.7 ± 0.2	0.28 - 2.18
	8	0.8 ± 0.1	0.28 - 1.47
	12	0.6 ± 0.2	0.14 - 1.60
	16	0.7 ± 0.2	0.10 - 2.01
	20	1.3 ± 0.3	0.36 - 3.26
2		1.3 ± 0.3	0.17 - 3.21
3		1.2 ± 0.4	0.41 - 3.99
4		1.3 ± 0.2	0.19 - 2.08
5		2.0 ± 1.0	0.14 - 10.45
6		0.8 ± 0.3	0.10 - 3.21
7		0.8 ± 0.2	0.19 - 2.88
8		0.5 ± 0.1	0.17 - 1.07
9		0.4 ± 0.1	0.10 - 1.36
10		0.5 ± 0.1	0.10 - 0.93
11		0.6 ± 0.1	0.17 - 1.56
12		0.7 ± 0.2	0.17 - 1.70
13		0.5 ± 0.1	0.14 - 0.93
14		0.9 ± 0.2	0.28 - 1.90
15		0.4 ± 0.1	0.11 - 0.74
-5		0.5 ± 0.1	0.33 - 0.70
-4		0.9 ± 0.3	0.18 - 3.42
-3		1.1 ± 0.3	0.15 - 2.90
-2		2.4 ± 0.5	0.40 - 5.27
-1		3.3 ± 0.5	1.07 - 5.53

increase in LH levels were noted beginning two days before the next cycle. A more descriptive characterization of the tonic LH levels (not including the elevated levels associated with the preovulatory surge) may be found in Figure 5, on page 47.

Figure 6 and Table 9 report the serum LH levels during the seasonal anestrous period. Basal levels with an overall mean of 0.71 ± 0.02 ng/ml, were maintained throughout the sampling period with no LH surges being observed.

Serum LH levels during the first 16 days postpartum are reported in Figure 7 and Table 10. Basal levels (0.32 ± 0.02 ng/ml) were maintained throughout the sampling period with no LH surges being observed.

Mean postpartum LH levels, which reflect the activity of the LH tonic system were significantly lower ($P < 0.01$) than mean seasonal anestrous LH levels, even though both exhibited basal levels throughout the sampling period. Tonic LH levels (basal) in the cyclic doe were found to be significantly higher ($P < 0.05$) than tonic LH levels recorded in seasonally anestrus or postpartum does.

Serum Luteinizing Hormone Response to GnRH Treatment During the Breeding Season, Seasonal Anestrus, and Early Postpartum Period

Figures 8, 9, 10, and Tables 11, 12, and 13, summarize the data obtained on the LH responses to two doses of 100 ug GnRH given at 0 and 3 hours. This treatment was administered to cyclic does on day

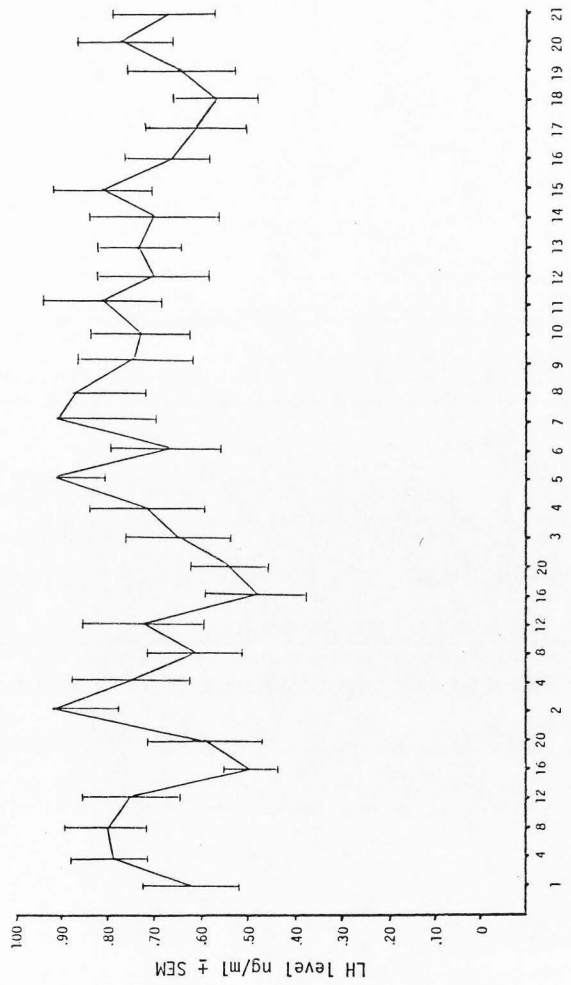

LH level ng/ml ± SEM
100
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
1 4 8 12 16 20 2 4 8 12 16 20 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Day of the sampling period

Table 9. Mean caprine serum LH levels on 21 consecutive days during the seasonal anestrous period (May 10-30, 1982), n=10.

Day of the sampling period			
Day	Hour	LH level ng/ml ± SEM	Range ng/ml
1	0	0.62 ± 0.10	0.13 - 0.87
	4	0.79 ± 0.09	0.28 - 1.25
	8	0.80 ± 0.09	0.43 - 1.24
	12	0.75 ± 0.11	0.28 - 1.49
	16	0.49 ± 0.06	0.17 - 0.87
	20	0.59 ± 0.12	0.15 - 1.13
2	0	0.92 ± 0.16	0.26 - 1.88
	4	0.75 ± 0.13	0.28 - 1.34
	8	0.61 ± 0.10	0.22 - 1.19
	12	0.72 ± 0.13	0.13 - 1.45
	16	0.48 ± 0.11	0.15 - 1.21
	20	0.54 ± 0.08	0.08 - 0.87
3		0.64 ± 0.11	0.08 - 1.20
4		0.71 ± 0.12	0.13 - 1.24
5		0.91 ± 0.11	0.36 - 1.46
6		0.67 ± 0.12	0.19 - 1.49
7		0.91 ± 0.22	0.28 - 2.59
8		0.88 ± 0.17	0.22 - 1.93
9		0.74 ± 0.13	0.23 - 1.39
10		0.73 ± 0.11	0.45 - 1.46
11		0.81 ± 0.13	0.15 - 1.48
12		0.70 ± 0.12	0.08 - 1.31
13		0.73 ± 0.09	0.24 - 1.27
14		0.70 ± 0.14	0.21 - 1.68
15		0.81 ± 0.11	0.30 - 1.34
16		0.67 ± 0.09	0.31 - 1.01
17		0.61 ± 0.11	0.13 - 1.08
18		0.57 ± 0.09	0.06 - 1.10
19		0.64 ± 0.12	0.23 - 1.50
20		0.77 ± 0.11	0.23 - 1.42
21		0.68 ± 0.11	0.30 - 1.37

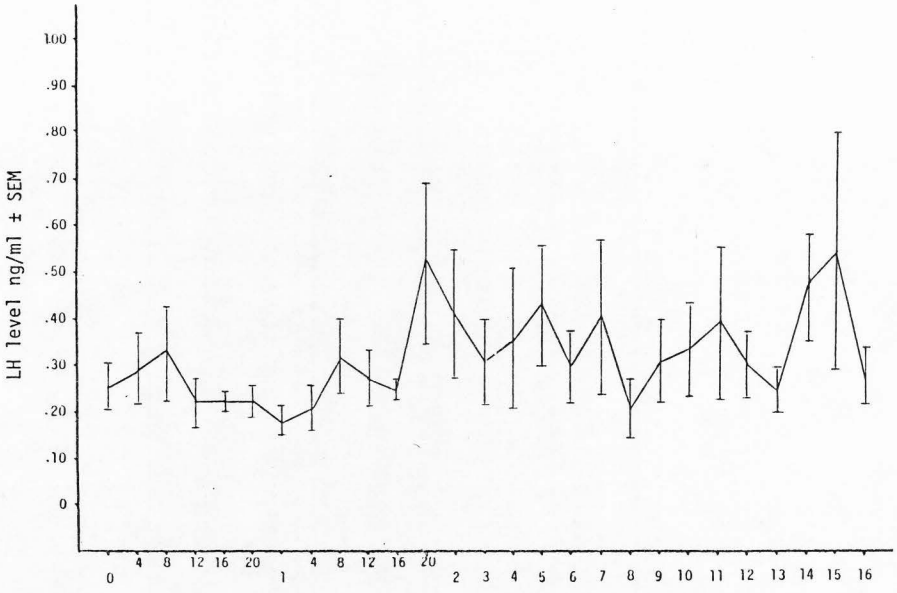
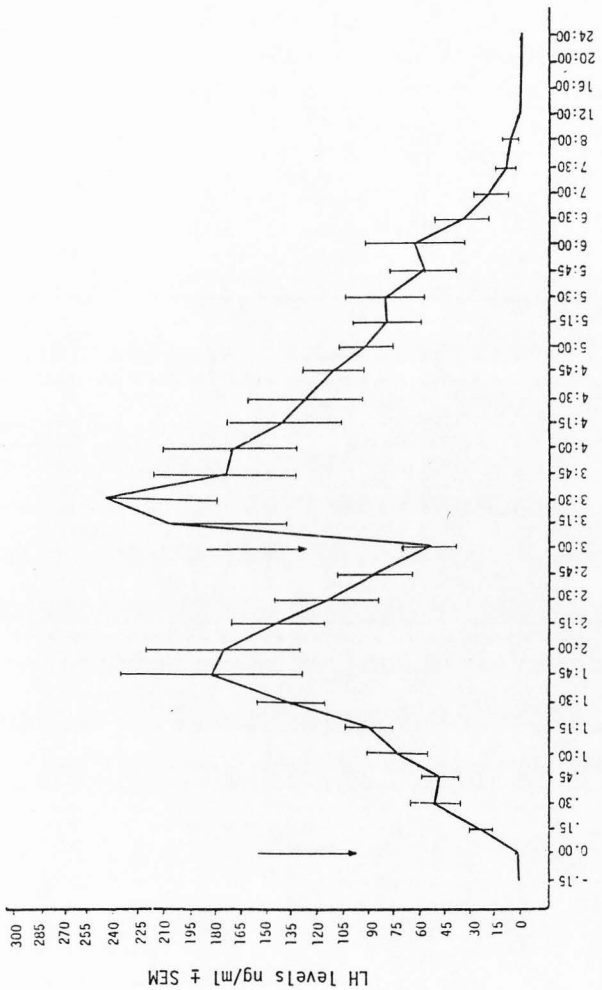

LH level ng/ml ± SEM
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
0 4 8 12 16 20 1 4 8 12 16 20 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Days Postpartum, Day 0 = Day of Parturition

Table 10. Mean caprine serum LH levels during the early postpartum period (May 19 - June 7, 1982). Sampling was initiated within six hours of parturition, n=9. Day 0 = day of parturition (all does were lactating).

Days Postpartum			
Day	Hour	LH level ng/ml ± SEM	Range ng/ml
0	0	0.26 ± 0.05	0.09 - 0.60
	4	0.29 ± 0.08	0.06 - 0.70
	8	0.33 ± 0.10	0.09 - 0.97
	12	0.22 ± 0.04	0.09 - 0.52
	16	0.22 ± 0.02	0.10 - 0.30
	20	0.22 ± 0.03	0.12 - 0.37
1	0	0.19 ± 0.03	0.01 - 0.35
	4	0.21 ± 0.04	0.01 - 0.41
	8	0.32 ± 0.08	0.11 - 0.86
	12	0.28 ± 0.06	0.08 - 0.59
	16	0.25 ± 0.02	0.13 - 0.34
	20	0.53 ± 0.17	0.07 - 1.45
2		0.41 ± 0.13	0.18 - 1.45
3		0.31 ± 0.09	0.11 - 0.97
4		0.36 ± 0.15	0.01 - 1.56
5		0.43 ± 0.13	0.06 - 1.25
6		0.30 ± 0.08	0.07 - 0.93
7		0.41 ± 0.17	0.13 - 1.76
8		0.21 ± 0.05	0.01 - 0.47
9		0.31 ± 0.09	0.01 - 0.57
10		0.34 ± 0.10	0.01 - 0.59
11		0.40 ± 0.17	0.08 - 1.74
12		0.31 ± 0.08	0.01 - 0.75
13		0.25 ± 0.05	0.01 - 0.50
14		0.48 ± 0.12	0.16 - 0.97
15		0.55 ± 0.26	0.10 - 1.53
16		0.28 ± 0.06	0.18 - 0.38


LH levels ng/ml ± SEM
300
285
270
255
240
225
210
195
180
165
150
135
120
105
90
75
60
45
30
15
0
-.15
0.00
.15
.30
.45
1:00
1:15
1:30
1:45
2:00
2:15
2:30
2:45
3:00
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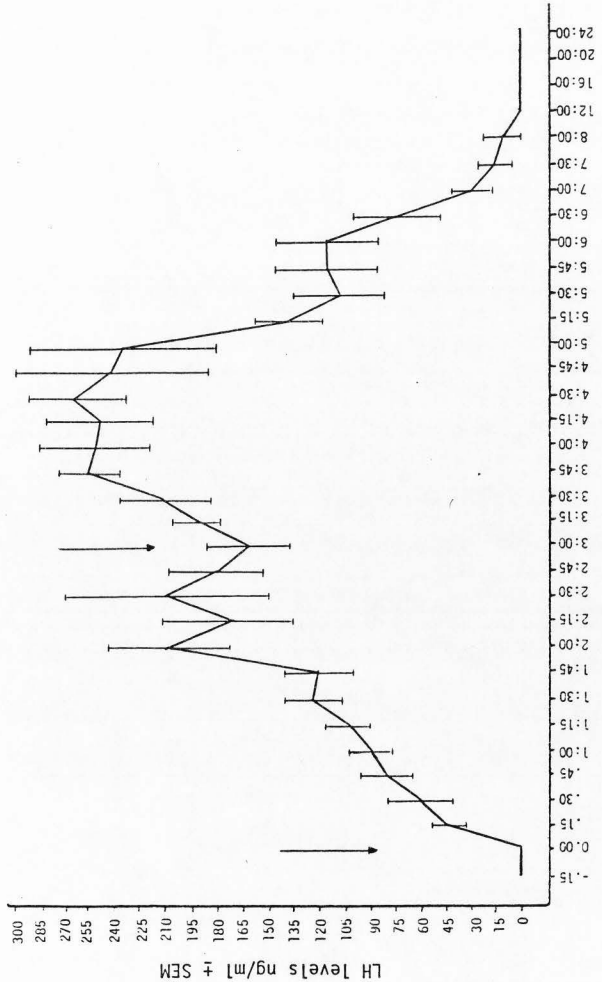
4:00
4:15
4:30
4:45
5:00
5:15
5:30
5:45
6:00
6:30
7:00
7:30
8:00
12:00
16:00
20:00
24:00
Time (in reference to the 1st GnRH injection)

Table 11. Mean caprine serum LH levels during the breeding season (January 21-22, 1982), following two injections of 100 µg GnRH (a = time of 1st injection) (b = time of 2nd injection), n=5. All does were in late luteal phase (days 16-17).

	Time (in reference to the 1st GnRH injection)	Serum LH levels ng/ml ± SEM	Range ng/ml
	-.15	0.40 ± 0.20	0.10 - 1.08
a	0.00	0.15 ± 0.05	0.10 - 0.36
	.15	23.31 ± 6.25	7.29 - 38.92
	.30	50.70 ± 14.33	20.65 - 91.60
	.45	47.82 ± 10.58	22.96 - 79.90
	1:00	73.15 ± 18.91	41.38 - 132.57
	1:15	90.10 ± 14.55	60.55 - 128.54
	1:30	135.57 ± 20.91	82.38 - 185.65
	1:45	182.96 ± 54.56	71.78 - 383.97
	2:00	175.95 ± 43.02	104.72 - 333.17
	2:15	144.64 ± 25.84	69.25 - 211.40
	2:30	113.07 ± 29.16	60.90 - 224.52
	2:45	86.22 ± 22.70	35.50 - 163.34
b	3:00	55.25 ± 14.90	23.87 - 110.86
	3:15	208.30 ± 69.15	76.87 - 468.83
	3:30	242.96 ± 63.96	100.23 - 414.93
	3:45	174.70 ± 41.76	73.20 - 296.07
	4:00	170.67 ± 39.55	81.13 - 298.49
	4:15	140.26 ± 32.98	42.95 - 240.96
	4:30	128.52 ± 34.00	33.86 - 234.13
	4:45	110.32 ± 19.16	44.55 - 155.10
	5:00	91.95 ± 17.56	30.11 - 134.98
	5:15	79.58 ± 21.41	20.65 - 140.70
	5:30	80.74 ± 24.16	13.35 - 138.10
	5:45	59.18 ± 20.43	4.69 - 103.19
	6:00	62.89 ± 29.32	3.89 - 161.63
	6:30	34.34 ± 16.60	1.06 - 84.20
	7:00	18.52 ± 9.16	0.10 - 40.53
	7:30	9.07 ± 6.07	0.10 - 32.65
	8:00	5.91 ± 3.08	0.10 - 14.24
	12:00	0.22 ± 0.07	0.10 - 0.46
	16:00	0.19 ± 0.04	0.10 - 0.32
	20:00	0.26 ± 0.09	0.10 - 0.49
	24:00	0.14 ± 0.04	0.10 - 0.30


LH levels ng/ml ± SEM
300
285
270
255
240
225
210
195
180
165
150
135
120
105
90
75
60
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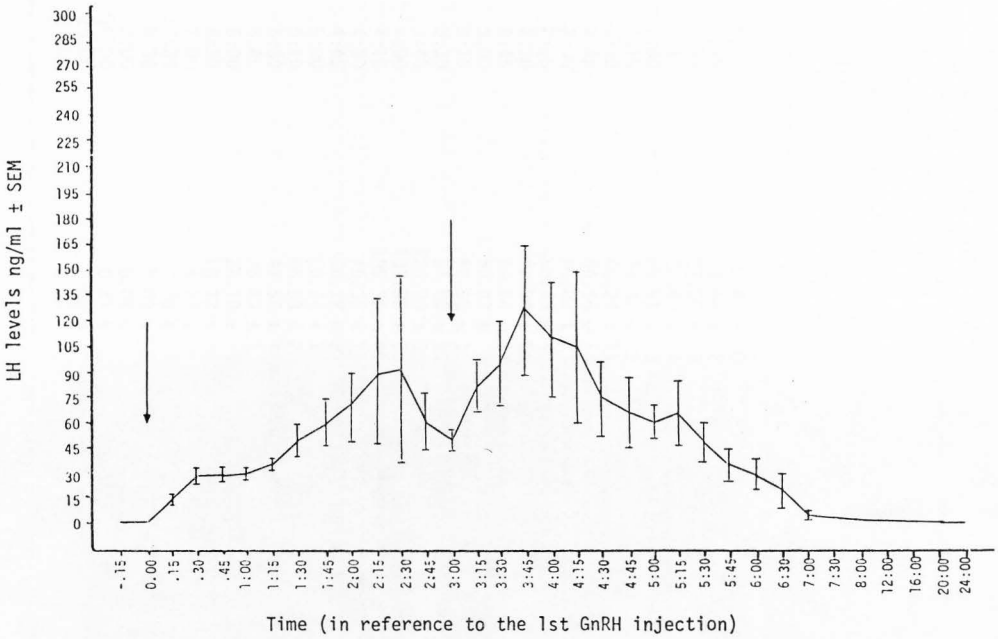
5:45
6:00
6:30
7:00
7:30
8:00
12:00
16:00
20:00
24:00
Time (in reference to the 1st GnRH injection)

Table 12. Mean caprine serum LH levels during the seasonal anestrous period (June 8-9, 1982), following two injection of 100 µg GnRH (a = time of 1st injection, b = time of 2nd injection), n=5.

Time (in reference to the 1st GnRH injection)		Serum LH levels ng/ml ± SEM	Range ng/ml
	-.15	0.25 ± 0.06	0.10 - 0.40
a	0.00	0.37 ± 0.21	0.10 - 1.19
	.15	44.67 ± 9.60	23.05 - 72.79
	.30	60.39 ± 19.75	33.25 - 136.21
	.45	80.59 ± 15.50	50.90 - 136.21
	1:00	89.17 ± 13.73	58.38 - 123.14
	1:15	102.39 ± 13.09	64.15 - 142.70
	1:30	123.91 ± 17.42	83.93 - 188.97
	1:45	120.88 ± 20.29	73.83 - 180.34
	2:00	209.38 ± 41.38	122.11 - 333.17
	2:15	171.84 ± 36.44	118.62 - 312.15
	2:30	209.71 ± 59.74	118.39 - 414.18
	2:45	179.90 ± 27.16	113.04 - 242.73
b	3:00	162.03 ± 23.90	98.12 - 239.22
	3:15	190.21 ± 12.48	151.26 - 225.84
	3:30	210.60 ± 26.02	144.07 - 286.14
	3:45	254.21 ± 20.35	203.40 - 320.88
	4:00	250.41 ± 39.30	155.89 - 368.06
	4:15	247.04 ± 33.04	229.24 - 349.81
	4:30	266.19 ± 30.67	208.67 - 353.33
	4:45	242.58 ± 56.36	142.03 - 451.22
	5:00	235.89 ± 55.00	107.51 - 435.04
	5:15	138.86 ± 22.07	92.53 - 199.61
	5:30	109.74 ± 26.47	97.09 - 166.81
	5:45	115.50 ± 32.44	63.19 - 235.80
	6:00	115.91 ± 29.54	49.81 - 214.19
	6:30	75.71 ± 24.40	25.37 - 159.12
	7:00	31.00 ± 13.47	8.68 - 82.64
	7:30	18.22 ± 10.79	3.90 - 61.15
	8:00	13.74 ± 10.36	1.47 - 55.05
	12:00	0.57 ± 0.24	0.14 - 1.50
	16:00	0.34 ± 0.16	0.10 - 0.95
	20:00	0.21 ± 0.07	0.10 - 0.45
	24:00	0.14 ± 0.12	0.10 - 0.19


LH levels ng/ml ± SEM
300
285
270
255
240
225
210
195
180
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4:45
5:00
5:15
5:30
5:45
6:00
6:30
7:00
7:30
8:00
12:00
16:00
20:00
24:00
Time (in reference to the 1st GnRH injection)

Table 13. Mean caprine serum LH levels during the postpartum period (June 4-5, 1982), following two injections of 100 µg GnRH (a = time of 1st injection) (b = time of 2nd injection), n=5. All does were 15-17 days postpartum.

Time (in reference to the 1st GnRH injection)		Serum LH levels ng/ml ± SEM	Range ng/ml
	-.15	0.88 ± 0.81	0.03 - 4.11
a	0.00	0.47 ± 0.37	0.06 - 1.93
	.15	13.64 ± 2.42	6.69 - 20.21
	.30	27.56 ± 5.74	14.86 - 47.25
	.45	28.60 ± 4.91	20.31 - 47.45
	1:00	29.51 ± 3.72	20.46 - 40.61
	1:15	34.37 ± 3.14	27.79 - 43.25
	1:30	48.23 ± 11.80	20.65 - 91.29
	1:45	59.56 ± 14.05	37.75 - 114.85
	2:00	69.83 ± 21.75	44.11 - 156.69
	2:15	88.48 ± 43.42	39.79 - 261.77
	2:30	92.84 ± 55.84	26.52 - 315.64
	2:45	60.84 ± 17.81	31.97 - 130.24
b	3:00	50.07 ± 7.23	36.82 - 75.98
	3:15	82.33 ± 15.10	48.76 - 125.79
	3:30	94.50 ± 25.14	53.56 - 184.56
	3:45	126.29 ± 39.91	42.02 - 268.03
	4:00	109.80 ± 33.06	49.81 - 232.48
	4:15	105.36 ± 45.92	33.58 - 283.76
	4:30	75.39 ± 22.27	34.20 - 159.95
	4:45	66.22 ± 22.88	28.89 - 155.89
	5:00	60.24 ± 11.82	31.77 - 93.16
	5:15	66.58 ± 20.42	24.84 - 135.59
	5:30	47.58 ± 13.48	18.55 - 94.43
	5:45	35.49 ± 10.03	10.94 - 68.33
	6:00	28.10 ± 9.74	8.10 - 64.65
	6:30	18.17 ± 9.61	3.09 - 55.95
	7:00	4.24 ± 1.93	1.18 - 11.73
	7:30	1.36 ± 0.48	0.29 - 3.10
	8:00	1.09 ± 0.59	0.25 - 3.40
	12:00	0.08 ± 0.01	0.03 - 0.12
	16:00	0.21 ± 0.16	0.02 - 0.86
	20:00	0.08 ± 0.01	0.06 - 0.09
	24:00	0.12 ± 0.06	0.02 - 0.30

15-17 of the estrous cycle, seasonally anestrous does in mid anestrus and lactating does 15-17 days postpartum. The general pattern of LH secretion following two injections of 100 µg GnRH at 0 and 3 hours can be characterized as follows: low tonic LH levels (mean ± SEM = 0.51 ± 0.27 ng/ml) were present in all does, regardless of the reproductive phase, prior to the initial injection of GnRH. Upon administration of the initial GnRH injection serum LH levels increased to 182.96 ± 54.56, 209.38 ± 41.38, and 92.84 ± 55.84 ng/ml, these peak levels were recorded at 114 ± 4, 135 ± 7, and 135 ± 11 minutes post injection in the cyclic, seasonally anestrus, and postpartum does, respectively. Response to the second injection of 100 µg releasing hormone was more rapid and heightened, providing peaks of 242.96 ± 63.96, 254.20 ± 20.35, and 126.29 ± 39.91 ng/ml, these peak levels were recorded at 27 ± 3, 66 ± 14, and 51 ± 8 minutes post injection in the breeding season, seasonal anestrus, and postpartum groups, respectively. Serum LH levels had returned to baseline concentrations (similar to those recorded prior to the initial GnRH injection) by nine hours following the second injection in all three phases.

Statistically LH responses to GnRH were determined by comparing the area under the LH curve from the time of the initial GnRH injection until eight hours following the initial GnRH injection. The area under the curve is a reflection of the total LH released and is expressed as ng/ml x hour. The response of seasonally anestrous does to GnRH (1037.24 ± 88.7 ng/ml x hour) was significantly greater ($P<0.01$) than that shown by postpartum does (379.43 ± 111.7 ng/ml x hour). Seasonally anestrus

does also showed a greater response ($P < 0.05$) than cyclic animals (701.38 $\pm$ 117.9 ng/ml x hour) to GnRH. The response of cyclic does to GnRH was greater ($P < 0.058$) than the response shown by postpartum does. The response to the first injection of GnRH may be estimated by comparing the area under the LH curve from 0-3 hours (the time from the injection of the initial 100 µg GnRH until the second injection there hours later).

Cyclic and seasonally anestrous does showed no significant difference ($P < 0.05$) in response to the initial injection of 100 µg GnRH (272.04 $\pm$ 45.94 vs. 358.88 $\pm$ 49.17 ng/ml x hour, respectively). However, the response of both the cyclic and seasonally anestrous does were greater ($P < 0.063$) than that recorded for the postpartum does (139.38 $\pm$ 41.57 ng/ml x hour). The time required to attain peak LH levels levels following the second GnRH injection was significantly less ($P < 0.01$) than the time required to reach peak LH levels following the first injection of GnRH, 128 $\pm$ 5 vs 48 $\pm$ 7 minutes, respectively. Peak levels following the second GnRH injection were higher than peak LH levels following the first injection of GnRH, but these data must be interpreted with caution because residual LH released following the first GnRH injection, may have supplemented the LH response to the second injection of GnRH.

Ovarian Responses to GnRH Treatment During The Breeding Season, Seasonal Anestrus, and Early Postpartum Period

These data are summarized in Table 14 on page 62. GnRH (100 µg) was administered in two doses at 0 and 3 hours on day 15-17 of the estrous cycle, postpartum period, and on day 30 of the progesterone

Table 14. Ovarian activity nine days following GnRH treatment, and in the mid-sampling period in untreated control does during three reproductive phases (breeding season, seasonal anestrus, and the early postpartum period).

Reproductive phase	Treatment	Number of animals	Number of does ovulating	Ovulation rate per doe ovulating	Number of does with follicles ≥6 mm	Number of follicles ≥6 mm per doe having follicles ≥6 mm
Cyclic	Control	10	10/10	1.4	9/10	2.33
	GnRH	5	5/5	2.0	2/5	1.0
Seasonal Anestrus	Control	10	0/10	---	1/10	1.0
	GnRH	5	2/5	1.5	1/5	1.0
Postpartum	Control	9	0/9	---	3/9	1.33
	GnRH	5	0/5	---	0/5	---

sampling period in the seasonally anestrous does. Four aspects of ovarian response are considered, and are as follows: (1) The number of does ovulating, (2) Ovulation rate per doe ovulating, (3) The number of does with follicles ≥6 mm, (4) The number of follicles ≥6 mm per doe having follicles ≥6 mm. As expected, all cyclic does not receiving GnRH ovulated and exhibited a high level of follicular activity. Seasonal anestrus and postpartum animals showed no ovulation response and a reduced level of follicular activity which was significantly less ($P < 0.025$) than the response shown in cyclic animals.

GnRH treated animals during the breeding season responded with all five animals ovulating. Each doe ovulating had an average of two ovulation points which was higher ($P < 0.10$) than cyclic control does (1.4). These data showed a significantly higher ($P < 0.05$) number of does possessing follicles ≥6 mm in the cyclic control group than the cyclic GnRH group.

GnRH treated does of the seasonal anestrous group showed a higher ($P < 0.05$) number of does ovulating as compared with control seasonally anestrous does. Postpartum GnRH treated animals showed no response in any of the four aspects of ovarian activity.

Pituitary LH Concentrations During the Breeding Season, Seasonal Anestrous, and Early Postpartum Period

Because of high non-specific binding in the radioimmunoassay, the concentrations of pituitary LH are considered only as estimates of the actual LH values, nevertheless, trends observed are considered to be real. Mean pituitary LH concentrations (± SEM) were 1711 ± 378,

2069 ± 265 and 3542 ± 398 ug/g tissue, in the postpartum seasonal anestrous and breeding season animals, respectively. In the ewe, pituitary LH concentrations are reported to be less than values obtained in these data, but the postpartum concentration is consistently the lowest and the pituitary LH concentration in cyclic animals is consistently the highest (Jenkin et al., 1977; Roche et al., 1970; Chakraborty et al., 1974).

DISCUSSION AND CONCLUSIONS

The estrous cycle length of the goats used in this research was found to be between 18 and 24.5 days with a mean of 19.78 ± 0.12 days. Short and long cycles are also common and should not be considered abnormal (Prasad and Bhattacharyya, 1979). Romm in 1979, reported one doe with a consistent cycle length of ten days, this doe was bred successfully during a regular cycle and was considered to have "normal" endocrine function. It is quite possible that many of the long cycles, since they are commonly multiples of an average length cycle are manifestations of an ovulation without estrus.

Progesterone levels were significantly different during each of the three reproductive phases considered. During the breeding season high progesterone levels indicative of luteal function were present. The presence of corpora lutea on the ovaries of does during the breeding season was confirmed by laparoscopy. Throughout the sampling period in this study, the seasonal anestrus and early postpartum period were characterized by reduced progesterone levels, 0.65 ± 0.03 and 0.30 ± 0.02 ng/ml, respectively. Laparoscopic observations of the ovaries of seasonally anestrus and postpartum does revealed that no corpora lutea were present in any of the animals. The reason(s) for significantly higher ($P < 0.01$) levels of progesterone in the seasonally anestrous does as compared to the postpartum animals (0.65 ± 0.03 vs. 0.30 ± 0.02 ng/ml) are unknown. Assuming ovaries devoid of corpora lutea do not produce significant levels of serum

progesterone an extra ovarian source of progesterone might be postulated to account for these differences.

The LH surge system was demonstrated to be operational only during the breeding season as reported by other researchers (Romm, 1979; Kakusya, 1979). Peak LH surge values in the estrous or cyclic doe, as reported herein, are similar to those reported by Romm (1979). Kakusya (1979), reported maximum LH surge values of 20.1 $\pm$ 0.5 ng/ml. The literature reports a great deal of variation in peak LH values in the ewe but generally they are reported to be between 50 and 200 ng/ml (Pant et al., 1976; Pant et al., 1972; Goding et al., 1969). The anestrous and postpartum period in sheep are characterized by the absence of LH surges (Legan and Karsch, 1979; Kann et al., 1977; Wright et al., 1981) which are postulated to be dependent upon the effectiveness of estradiol negative feedback on tonic LH secretion (Legan et al., 1977; Wright et al., 1981). An approximate 48 hour sustained increase in tonic LH levels (4-5 fold higher than basal levels) has been shown to be a prerequisite to trigger the LH surge in the ewe (Legan and Karsch, 1979). No such sustained tonic LH levels were recorded in the seasonally anestrous or postpartum does.

Two different steroids are responsible for inhibition of the tonic LH release during the breeding season and seasonally anestrous periods in the ewe, respectively. Progesterone acts as the major inhibiting steroid on the tonic LH center during the breeding season while estradiol acts as the primary negative feedback steroid on tonic LH

secretion during the seasonally anestrous period (Karsch et al., 1977; Hauger et al., 1977; Legan et al., 1977). Estradiol has also been implicated as a potent negative feedback influence on tonic LH secretion in the postpartum ewe (Wright et al., 1981). Our data, consistent with those reported by Romm (1979) and Kakusya (1979) suggest a negative relationship between circulating progesterone and LH during the breeding season. This observation adds support to the thesis that in the goat, as well as the ewe, luteal levels of progesterone suppress the tonic LH pulse frequency (Karsch et al., 1977). To date, the literature does not report research to determine if estradiol is the primary negative feedback steroid on tonic LH secretion in the seasonally anestrus and/or postpartum does.

Mean postpartum basal LH levels, which reflect the activity of the LH tonic system, were significantly lower ($P<0.01$) than the mean basal LH levels in seasonally anestrous goats. Research in the sheep indicate that postpartum ewes exhibit a reduced sensitivity of the anterior pituitary to GnRH as compared to cyclic and seasonally anestrous ewes (Jenkin et al., 1977; Moss et al., 1980; Chamley et al., 1976). A recent publication (Crowder et al., 1982) reported that in the days following parturition, the number of GnRH receptors in the anterior pituitary declined ($P<0.05$), during the same interval when the response to GnRH was shown to progressively increase. This suggests that the number of GnRH receptors are not responsible for the progressive increase in the pituitary sensitivity to GnRH postpartum. Also the number of GnRH receptors in the postpartum ewes were as great or greater than the number found in ovariectomized or cyclic luteal phase

ewes. This finding sheds doubt on the idea that the relatively lower sensitivity of the pituitary to GnRH during the postpartum period could be accounted for by a decrease in the number of GnRH receptors postpartum relative to the breeding season.

Crowder et al. (1982) reported further that the GnRH induced release of LH and pituitary content of LH increased with time after parturition ($P < 0.05$) and were highly correlated ($r = 0.976$). Concentrations of hypothalamic GnRH did not change throughout the postpartum period. These data suggest that pituitary LH levels in the postpartum doe are lower than the levels of pituitary LH in seasonally anestrous and cyclic does. Indeed, pituitary LH concentrations recorded in this study are consistent with this hypothesis. These results could in part account for the lower tonic LH levels in postpartum animals as compared to seasonally anestrous does. Other factors may affect the tonic LH levels in the postpartum and seasonally anestrous goat. Wright et al. (1981) demonstrated a reduced intrinsic GnRH pulse frequency in ovariectomized postpartum ewes. The evidence for a negative feedback by estradiol on tonic LH secretion is well established in seasonally anestrous ewes (Legan et al., 1977; Legan and Karsch, 1979), and implicated in postpartum ewes. It is possible that the sensitivity of the tonic LH center is greater in postpartum does resulting in lower tonic LH levels postpartum, as compared to seasonally anestrous animals which may have a lower although still significant sensitivity to estradiol at the tonic LH level.

Data obtained in this study on the response of the anterior pituitary to GnRH are consistent with those reported in the ewe, namely that (1) there is a reduced sensitivity of the anterior pituitary to GnRH during the postpartum period as compared to the breeding season and seasonally anestrous period, and (2) there is an increase in sensitivity of the pituitary to a second injection of GnRH when the interval between the injections is three hours or less.

The observation that postpartum ewes have a reduced sensitivity to GnRH as compared to seasonally anestrous and cyclic does has been discussed previously in this section. It is consistent with data obtained in this study and in the ewe, to postulate that the goat becomes less responsive to GnRH during the postpartum period because of decreased pituitary LH levels. LH receptors have been shown to be associated with secretory granules in the anterior pituitary (Nett et al., 1981). It is conceivable that there is a decrease in the releasable LH within secretory granules in the postpartum doe. We may further suggest that the response to GnRH during the postpartum period is independent of changes in the number of GnRH receptors or levels of hypothalamic GnRH postpartum (Crowder et al., 1982). Moss et al. (1980) suggests that a constant percentage (47.1 $\pm$ 3.2 percent) of the LH contained in the pituitary cells was released in response to a maximally stimulatory dose of GnRH throughout the postpartum period. Therefore, more LH was released later in the postpartum period because more LH was contained in the pituitary, not because the ability of the gonadotroph to respond to GnRH had changed. Again, a

decreased LH content within the secretory granules in the anterior pituitary could possibly explain this observation.

It has been shown that GnRH responsiveness is not related to the incidence of or interval to the first postpartum estrus in the ewe (Wright et al., 1980). Full recovery of the sensitivity of the anterior pituitary is obtained well before the first ovulation, therefore, factors other than the reduced sensitivity of the pituitary to GnRH are involved in the acyclic postpartum period in ewes (Wright et al., 1981) and most likely in the doe.

We also found an increased sensitivity of the pituitary to a second injection of GnRH when the interval between injections were three hours or less. As reported earlier in this research, the time from the first GnRH injection until peak plasma LH levels were reached were significantly different ($P < 0.01$) than the time required to attain peak LH levels following the second GnRH injection (128 $\pm$ 5 vs. 48 $\pm$ 7 minutes, respectively). Peak levels following the second GnRH injection were higher than those attained following the first injection of GnRH, but these data are difficult to interpret since the peak levels attained following the second injection of GnRH were higher than expected because residual serum LH, released following the first injection of GnRH, supplemented the LH response to the second GnRH injection. Crighton and Foster (1976) reported that the response to a second injection of GnRH when administered 1.5 hours after the first caused a further increase in LH concentration over that obtained following

the first injection. When the second injection was administered three hours after the first, there was no significant difference between the responses, as judged by the area under the LH curve, to the two injections, although the time to reach the maximal LH concentration was shorter and the height of the LH peak was greater in each animal following the second injection. GnRH has been found to participate in the regulation of its own receptors in the ewe. Nett et al. (1981) reported that the number of GnRH receptors (moles receptor/mg pituitary x 10^{-16}) were 1.96 ± 0.38, 2.72 ± 0.37, 2.50 ± 0.58, 3.85 ± 0.71, 1.41 ± 0.14, and 1.00 ± 0.10 after 0, 1, 2, 4, 12, and 24 hours of infusion of GnRH, respectively. It is possible that GnRH may participate in the regulation of its own receptors in the goat since the results obtained in all three reproductive phases in this study on the sensitivity of the pituitary to two injections of GnRH are consistent with those reported in the ewe. Recent findings seem to suggest that changes in the sensitivity of the anterior pituitary toward GnRH is modified by ovarian steroids which act in two ways, (1) to reduce pituitary LH levels following chronic steroid exposure, and (2) they may regulate the number of GnRH receptors, or affinity of these GnRH receptors toward LH following an acute steroid exposure. This second regulatory system mentioned, may be responsible for the greater response ($P < 0.05$) of the anterior pituitary to GnRH in seasonally anestrus as compared to cyclic does.

Ovarian response following GnRH treatment was recorded in the breeding season, seasonal anestrous, and postpartum period. Several interesting results were obtained: (1) there was a significant reduction in the number of does ovulating ($P < 0.05$) in the seasonally

anestrous and postpartum groups as compared to cyclic does, (2) during the seasonal anestrous period GnRH treatment induced a significant increase ($P < 0.05$) in the number of does ovulating, (3) there was a reduction ($P < 0.05$) in the number of does having follicles ≥ 6 mm in the GnRH treated does as compared to controls during the breeding season, (4) postpartum does were found to be completely unresponsive.

Previous research has shown a reduced ovarian response to GnRH injections in the anestrous and postpartum ewe as compared to cyclic ewes (Rippel et al., 1974; Restall et al., 1977; McNeilly et al., 1981). The reduced LH release by the pituitary in GnRH treated postpartum does may be responsible for the lack of ovarian response in this reproductive phase, but our results indicate seasonally anestrous does respond with a greater ($P < 0.05$) LH release following a given dose of GnRH than did cyclic does. Reduced ovarian response to GnRH during the seasonal anestrous period is probably mediated at the ovarian level. It is evident from recent studies in the ewe that LH release in a pulsatile manner at a pulse frequency of approximately one pulse/hour is more critical in terms of ovarian response and corpus luteum function than one large peak of LH as is observed following a GnRH injection (McNatty et al., 1982). My results suggest the same may hold true in the doe.

GnRH administration induced a significantly greater ($P < 0.05$) number of treated does to ovulate as compared to controls during the seasonal anestrous period. Research in the ewe indicates that corpora lutea, induced in seasonally anestrous ewes by a single injection of GnRH have a greatly reduced ability to synthesize and secrete progesterone (McNeilly et al., 1981). It is postulated that insufficient

gonadotropin priming previous to the induced ovulation is responsible for the abnormal corpora lutea (McNeilly, 1980). Progesterone levels in the does induced to ovulate, by GnRH injection during seasonal anestrous, were not measured in this study.

My results showed a significant reduction in the number of does having follicles ≥6 mm in the GnRH treated does as compared to controls during the breeding season. Symons et al. (1974) reported that cyclic ewes injected with GnRH during the midluteal phase exhibited an LH surge at the time of GnRH injection as expected. However, this midcycle LH surge did not change the estrous cycle length of the animals since all ewes exhibited behavioral estrus at the regular time approximately one half estrous cycle length following GnRH treatment. It is possible that in such a circumstance a double peak of LH could occur, the GnRH induced peak expressed at the mid-cycle and a second peak approximately one half cycle later at the regular time of behavioral estrus. The significantly lower follicular activity of does treated with GnRH midcycle might be explained by the following hypothetical sequence of events: at the time of GnRH treatment the competent follicles would ovulate, a later wave of follicles present at the time of the normal preovulatory surge would also contain competent follicles capable of ovulating (Richards and Midgley, 1976). Presumably, these events could account for the relatively higher ovulation rate and lower follicular development in the cyclic ewes treated with GnRH at midcycle.

The postpartum does exhibited a complete lack of ovarian response to GnRH treatment, by the measures imposed. As shown earlier, pituitary responsiveness to GnRH is reduced during this period, this most probably being the result of reduced pituitary LH levels. It is also possible that there is a reduced response at the ovarian level to gonadotropins. My results are consistent with those obtained in the postpartum ewe demonstrating the hormonally refractory nature of the postpartum period.

Estimates of the pituitary LH concentration of does during the breeding season, seasonal anestrus, and early postpartum period are 3542 $\pm$ 398, 2069 $\pm$ 265, and 1711 $\pm$ 378 ug/g tissue, respectively. Significantly lower pituitary LH concentrations (as compared to concentrations in the seasonal anestrous and breeding season) are consistently reported in postpartum ewes. Chronically elevated progesterone and estradiol levels in the ewe have been shown to reduce pituitary LH concentrations significantly (Moss et al., 1981). Progesterone levels in the pregnant goat have been shown to be maintained at elevated levels (4.5 - 5.5 ng/ml, similar to midluteal progesterone levels as measured by these researchers) for the last 70-80 days of gestation (Thornburn and Schneider, 1971). Estradiol has also been shown to be elevated (relative to non-pregnant does) during the last 50 days of pregnancy with a significant increase in estradiol levels just previous to parturition. From this peak estradiol level at parturition, estradiol decreased progressively for 19 days postpartum (Jain et al., 1982). It is possible that the goat responds to the chronically elevated progesterone and estradiol levels during gestation with reduced pituitary LH levels.

At parturition elevated steroid levels are progressively removed, correlating with the progressive increase in LH response to GnRH throughout the postpartum period, making the proposed endocrine events of the postpartum doe similar to those observed in the ewe (Crowder et al., 1982).

SUMMARY

Female Spanish x Dairy cross goats were divided into three reproductive phases--estrous cycle (20), seasonal anestrous (20), and early postpartum (20). Each of these three groups of animals were further divided into three treatments--control (10), GnRH treated (5), and pituitary LH (5). Control animals were bled every four hours for 48 hours and thereafter daily for 16-21 days at selected times during the breeding season, seasonal anestrous, and early postpartum period. Sera obtained were analyzed by radioimmunoassay (RIA) for progesterone and LH. Five does in each reproductive phase were treated with GnRH (two doses of 100 μg at 0 and 3 hours). In GnRH treated animals, the serum was sampled 15 minutes prior to the first GnRH injection, at the time of the first GnRH injection and thereafter every 15 minutes for six hours, every 30 minutes for the next two hours, and every four hours for the final 16 hours. LH response was measured by RIA. The anterior pituitary gland was removed immediately after sacrifice from five animals during each of the three above mentioned reproductive phases and analyzed for LH concentration. Ovarian activity was also measured by laparoscopy in GnRH treated and control does by recording the number of does ovulating, ovulation rate per doe ovulating, number of does having follicles ≥6 mm, and the number of follicles ≥6 mm per doe having follicles ≥6 mm.

Progesterone levels in the breeding season reflected the waxing

and waning of the corpus luteum, with low levels (<1.5 ng/ml) at the time of estrus and for an additional 3-4 days. On day 3-4 of the cycle, progesterone levels began to increase reaching a high level which fluctuated between 6.12 ± 0.55 and 7.31 ± 0.6 ng/ml on day 6 to -4. A sharp drop in progesterone levels occurred on day -3 or -4 of the cycle, to the low levels measured at estrus.

Progesterone levels during the seasonal anestrous and the postpartum period were low throughout the sampling period, 0.65 ± 0.03 and 0.30 ± 0.02 ng/ml, respectively, and were significantly different ($P < 0.01$).

The LH surge mechanism was operational only in breeding season does, showing LH peaks of 187.86 ± 3.95 ng/ml an average of 13.2 ± 1.47 hours after the onset of estrus. Serum LH had returned to low levels (1.11 ± 0.13 ng/ml) by 48 hours post-estrus where they remained throughout the luteal phase. The inverse relationship between serum LH and progesterone suggest that progesterone is an inhibitor of tonic LH secretion. Serum LH levels during the seasonal anestrous and postpartum period were basal, 0.71 ± 0.02 and 0.32 ± 0.02 ng/ml, respectively, and reflect significant differences ($P < 0.01$) in tonic LH secretion. Tonic LH levels in the cyclic doe were found to be significantly higher ($P < 0.05$) than tonic LH levels in either seasonally anestrous or postpartum does.

GnRH (2 x 100 μg at 0 and 3 hours) was administered to cyclic does on day 15-17 of the estrous cycle, seasonally anestrous does in mid-anestrous and lactating does 15-17 days postpartum. Low tonic LH

levels (0.51 ± 0.27 ng/ml) were present in all does, regardless of reproductive phase, prior to the initial GnRH injection. Upon administration of GnRH serum LH levels increased to 182.96 ± 54.56, 209.38 ± 41.38, and 92.84 ± 55.84 ng/ml, these peak levels were reached at 114 ± 4, 135 ± 7, and 135 ± 11 minutes post-injection in the cyclic, seasonally anestrus, and early postpartum does, respectively. Response to the second injection of 100 µg releasing hormone was more rapid and heightened, providing peaks of 242.96 ± 63.96, 254.20 ± 20.35, and 126 ± 39.91 ng/ml, these peak levels were recorded at 27 ± 3, 66 ± 14, and 51 ± 8 minutes post injection in the breeding season, seasonal anestrous and postpartum groups, respectively. Serum LH levels had returned to basal levels (<1 ng/ml) in all three reproductive phases by nine hours following the second injection of GnRH. The first injection of GnRH sensitized the anterior pituitary to the second GnRH injection three hours later, since the serum LH response to the second GnRH injection was more rapid.
And responses of the postpartum animals was always reduced compared to the response of seasonally anestrous and cyclic animals. This reduced response of postpartum animals to GnRH is thought to be a manifestation of the lower pituitary LH concentration in postpartum animals 1711 ± 378 as compared to seasonally anestrous and cyclic does, 2069 ± 265 and 3542 ± 398 ug/g tissue, respectively.

There was a reduction ($P < 0.05$) in the number of does ovulating in the seasonally anestrous and postpartum does as compared to the cyclic GnRH treated groups. GnRH was found to increase ($P < 0.05$)

the number of does ovulating in the seasonal anestrous period, but postpartum does showed no response to GnRH. There was a reduction in the number of does having follicles ≥6 mm in the GnRH treated does as compared to controls during the breeding season.

This study clearly demonstrates the hormonally refractory nature of the postpartum period. It is probable that reduced responses to GnRH in postpartum does are a consequence of reduced pituitary LH stores. This study also provides evidence that progesterone is the primary negative influence on tonic LH secretion during the breeding season. Estradiol-17β is the major negative influence on tonic LH secretion in the ewe during the seasonal anestrous period. Further research to determine the affect of estradiol-17β on tonic LH secretion during seasonal anestrus in the goat is needed. Endocrine function in the parameters measured in this study are similar to responses in the ewe during the respective reproductive phases.

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