Changes in Serum Levels of LH, FSH, Prolactin, Testosterone, and Cortisol Associated with Season and Mating in Male Pygmy Goats

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Four male pygmy goats were used in a study designed to determine the effects of season on serum hormone (luteinizing hormone, follicle stimulating hormone, prolactin, testosterone, and cortisol) levels, testis size and libido, and the effects of mating on serum hormone profiles. Seasonal peaks were observed for prolactin in July, luteinizing hormone and follicle stimulating hormone in September, and testosterone in October. Luteinizing hormone peak frequency was greatest in September and was increased by mating activity in the months immediately preceding the breeding season. Scrotal circumference did not vary with season and libido showed no consistent seasonal pattern. Mating appeared to raise all hormone levels except during the months when these hormones were seasonally elevated. When episodic releases of luteinizing hormone occurred, they were associated with subsequent rises in serum testosterone levels. On some mating days, when episodic releases of luteinizing hormone were absent, changes in testosterone levels were highly correlated with changes in cortisol levels. It was concluded that both season and mating influence reproductive hormone levels in male pygmy goats.

Key words: male goats, season, mating effects, gonadotropins, prolactin, testosterone, cortisol, libido, scrotal circumference.

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The serum levels of hormones associated with reproduction, including luteinizing hormone (LH), follicle stimulating hormone (FSH), prolactin (PRL), and testosterone, vary with season in male sheep (Sanford et al, 1974a, 1976, 1978; Lincoln and Short, 1980), deer (Mirarchi et al, 1978; Schulte et al, 1981; Bubenik et al, 1982) and goats (Muduuli et al, 1979). Of these species, the goat has been studied the least. The only comprehensive study of seasonal changes in levels and secretion patterns of multiple hormones in male goats was done by Muduuli et al (1979) in the pygmy goat. Because the animals were not mature at the initiation of that study, additional data on more mature animals is desirable.

When rams are allowed to mate with estrous ewes and achieve multiple ejaculations, elevations in serum levels of LH, testosterone, and sometimes FSH have been noted (Sanford et al, 1974b, 1976, 1977; Moore et al, 1978; Yarney and Sanford, 1983). The stimulatory effect of mating on hormone levels in rams occurs at times of the year other than the peak of the breeding season and declines with prolonged periods of sexual activity (Sanford et al, 1974b, 1976, 1977).

The following study was designed to re-examine the effect of season and to determine the effect of mating activity on: 1) serum levels of LH, FSH, PRL, testosterone and cortisol, and 2) secretory patterns of selected hormones in male pygmy goats.

Materials and Methods

Animals and Treatment

Four male pygmy goats, 3 to 4 years of age, were housed as a group in a heated barn (temperature varied

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from 5 C in winter to 25 C in summer). Numerous windows in the barn allowed the animals to experience normal seasonal changes in photoperiod. Artificial lighting was normally used only during working hours (0800–1700 hours).

During the first week of each of 13 consecutive months, the animals were bled at 20-minute intervals for 6 hours (control day). During the next week, the animals were subjected to the same bleeding schedule while penned with estrous does (mating day). On mating days, two of the bucks were removed from the group pen and placed in adjacent pens in a separate area of the barn. Each pen contained an ovariectomized doe that had been treated with i.m. injections of steroids in oil (10 mg progesterone on days −7 and −5, 5 mg progesterone on day −3 and 225 μg estradiol-17β on day −1). At the end of the first day, each doe received 150 μg estradiol-17β to maintain estrus through the next day when the other two bucks were bled. On each mating day, the does were switched after the first 3 hours to provide additional sexual incentive for the bucks. The number of matings (mounts culminating in ejaculation) for the 6-hour period was recorded for each animal.

During the third week of each month, the animals were tranquilized using 1 ml Atravet (Ayerst, Montreal) injected i.m., and the scrotal circumferences were measured. All measurements were made by the same person.

The jugular blood samples, collected during the first and second weeks of each month, were obtained by venipuncture using 5-ml vacutainers. Samples were kept on ice and then refrigerated until serum was obtained by centrifugation. Serum pools representing the 6-hour collection period for each buck were prepared by combining equal volumes of serum from each sample. Pools and individual samples were frozen at −20 C until assayed for LH, FSH, PRL, testosterone, and cortisol.

Hormone Assays

Serum levels of LH, FSH, and PRL were determined by double antibody radioimmunoassays. When individual samples were assayed (LH only), all the samples collected from a single goat during the study were assayed together. Pools for all animals were assayed for each hormone in single assays.

Luteinizing hormone was measured by the method of Niswender et al (1969). The antibody (GDN #15) was used at an initial dilution of 1:100,000. LH values are expressed in terms of NIH-LH-S14. The sensitivity of the assay (95% B/Bo) was 0.1 ng/ml. The intraassay coefficient of variation for a pooled serum standard with a mean concentration of 1.5 ng/ml was 5.9%. This ovine LH assay has been used previously by this laboratory (Muduuli et al, 1979) and by Bon Durant et al (1981) for the quantitation of LH in goat serum or plasma.

Serum FSH concentrations were measured using the method of Cheng et al (1981). The values are expressed in terms of NIH-FSH-S12. The sensitivity (95% B/Bo) was 5 ng/ml. The intraassay coefficient of variation for duplicate samples with concentrations ranging from 38 to 42 ng/ml (mean = 40 ng/ml; n = 16) was 11.4%.

Serum PRL concentrations were determined as described by Sanford et al (1978), except that a different rabbit anti-ovine PRL serum was employed. There was no measurable cross reactivity with LH, FSH or TSH in the assay, but a 1% cross reaction with ovine growth hormone was observed. The antibody was used at an initial dilution of 1:60,000. Prolactin values are expressed in terms of NIH-PRL-S12. The sensitivity of the single assay performed (95% B/Bo) was 1 ng/ml. The intraassay coefficient of variation for duplicate samples ranging in concentration from 30 to 35 ng/ml (mean = 32.3 ng/ml; n = 12) was 6.9%.

The assays for FSH and prolactin were considered acceptable for estimating the levels of these hormones in goat serum since parallelism of serum curves and ovine standard curves were demonstrated and ovine hormone added to goat serum was recovered quantitatively.

Serum testosterone was determined as described by Yarney and Sanford (1983). The assay sensitivity (95% B/Bo) was 0.4 to 1.0 ng/ml. The cross-reactivity with cortisol in this assay was 0.1%. The intraassay coefficient of variation for a pooled serum sample with a mean concentration of 5.5 ng/ml was 4.6%.

The radioimmunoassay procedure for cortisol employed an antibody provided by Dr. N. C. Rawlings, University of Saskatchewan, Saskatoon, Canada. Information provided with the antibody indicated cross reactions of ≤1% with dehydroepiandrosterone, pregnenolone, testosterone, estradiol-17α, estradiol-17β, and cholesterol. The cross reaction with progesterone was 10%. This was not considered a problem when assaying serum from males. The antibody was used at an initial dilution of 1:750.

Serum samples (0.2 ml) or standards (0.2 ml) in phosphate-buffered saline (PBS) containing 0.1% gelatin were added to 12 × 75-mm glass tubes. Charcoal-stripped sheep serum (0.2 ml) was added to the tubes containing standards, and an equal volume of PBS was added to all unknown tubes. One milliliter of ethanol was added to each tube; the tubes were vortexed and then centrifuged for 10 minutes at room temperature. The supernatant was decanted into another 12 × 75-mm tube and evaporated to dryness under a stream of nitrogen in a 40 C water bath. The residue was dissolved in 1.2 ml PBS and duplicate 0.5 ml aliquots were transferred to a 12 × 75-mm tube. Antibody (0.1 ml) and hydrocortisone-1,2,6,7-^{3}H (New England Nuclear Corporation, Boston, MA) (0.1 ml, 30,000 cpm) were added. After vortexing, the tubes were incubated overnight at 4 C. Separation of free from bound hormone was achieved using dextran-coated charcoal as described for the testosterone method (Yarney and Sanford, 1983), except that the incubation period after addition of the charcoal was reduced to 10 minutes.

The sensitivity of the assay (95% B/Bo) was < 2 ng/ml. The intraassay coefficient of variation for a pooled serum sample with a mean concentration of 15.8 ng/ml was 5.5%.

Statistics

The effects of mating and month of the year on hormone concentrations in serum pools and on frequency of LH peaks were determined by analysis of variance.

LH peaks were arbitrarily defined as any rise of 2 ng/ml or more followed by at least one declining value. Values for LH peak frequency were transformed to $\sqrt{x} + 1/2$ for analysis. Differences between months for number of matings and scrotal circumference were determined by the Student-Newman-Keuls' test. Simple correlations between cortisol and testosterone concentrations were calculated for all goats on mating days in January and March.

Results

Mating Performance, Testicular Size, and Testosterone Levels

Data for scrotal circumference, number of matings/6 hours and serum testosterone concentration are shown in Fig. 1. Sex drive as measured by number of matings/6 hours did not change significantly from June through January. However, performance in February was lower ($P < 0.05$) than that observed in the previous June or November. During the last 2 months of the study, sex drive was reduced (May was lower than the previous June and the final month was lower than the previous June, October or November ($P < 0.05$)). Although scrotal circumference did not vary significantly over the year, serum testosterone levels were elevated during the fall months (month, $P < 0.01$). Testosterone levels on mating days were higher than on control days (mating, $P < 0.01$). The mating-induced elevations in testosterone levels appeared to be restricted to the months before and after the seasonal rise in serum testosterone, although the interaction of mating with month was not significant.

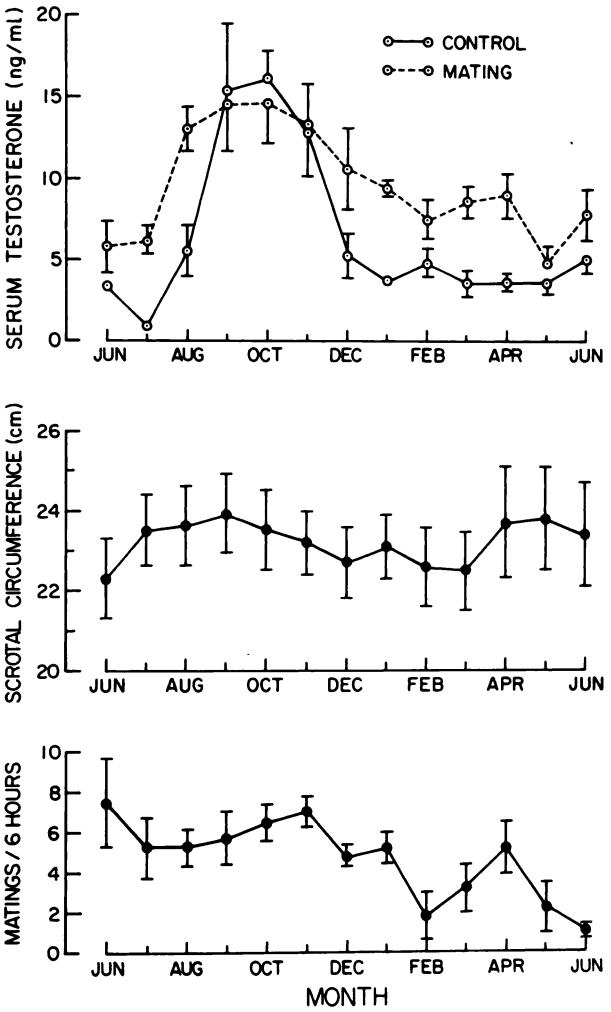

Fig. 1. Serum testosterone concentrations on control and mating days, scrotal circumference and number of matings/6 hours in male pygmy goats during 13 consecutive months. Values are means ± SE (n = 4). Standard errors not shown were too small to present graphically.

Serum Levels of LH, FSH, PRL, and Cortisol

The serum levels of LH, FSH, and PRL varied ($P < 0.01$) with season and were elevated ($P < 0.01$) on mating days (Fig. 2). The effect of mating on serum levels of LH was noted before the seasonal peak in September and again after the return to seasonal low levels in mid-winter (mating × month, $P < 0.01$). The serum levels of FSH tended to follow the same pattern, but the interaction was not significant. Prolactin levels appeared to be elevated by mating except in May and in July, when the seasonal peak for this hormone was observed (mating × month, $P < 0.01$). The most marked effects of mating were noted in October and November.

Serum cortisol levels were elevated by mating ($P < 0.01$) and varied with season (month, $P < 0.05$). The highest monthly values were noted at the beginning and end of the study in the month of June. During the first June, mating markedly elevated cortisol, while a year later control-day values were elevated (mating × month, $P < 0.01$).

LH Secretion Pattern

The results of assaying individual serum samples for LH revealed that LH concentrations were low (near or below the sensitivity of the assay) for most animals during the winter and spring months. Although, in some animals, mating appeared to elevate LH, this generally appeared to be due to a slight rise in baseline values with no

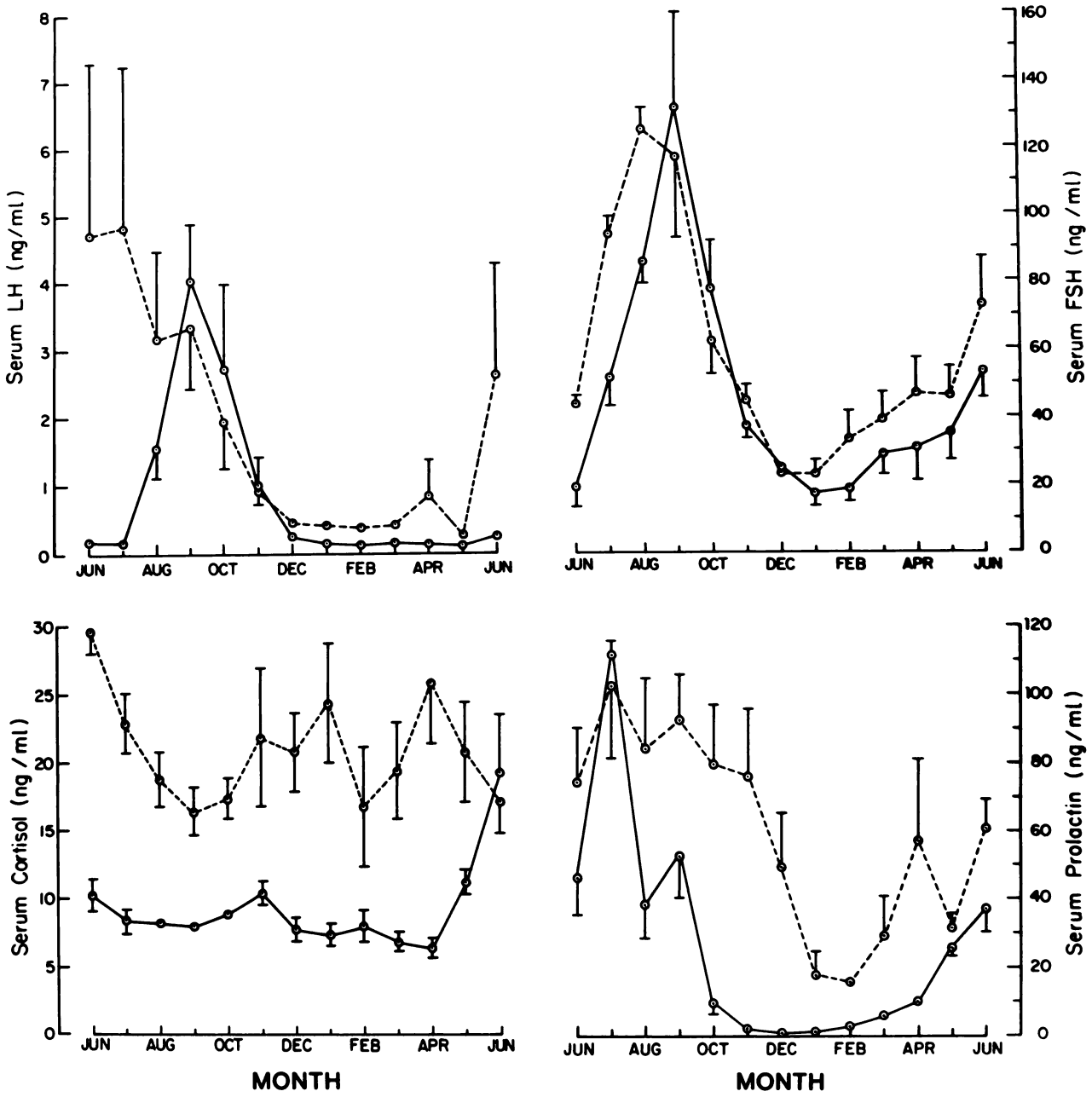

Fig. 2. Serum concentrations of LH, FSH, cortisol, and PRL in male pygmy goats on control (O——O) and mating (O- - -O) days during 13 consecutive months. Values represent means ± SE. Standard errors not shown were too small to present graphically.

episodic releases of LH being evident during the 6 hours of sampling. During the summer, when mating produced large elevations in LH levels, the pattern of secretion was characterized by large episodic releases of hormone. In some cases, several episodic releases appeared to have occurred in rapid succession, resulting in partial fusion of the individual peaks, and consequently the apparent baseline was markedly elevated. Figure 3 shows data from one animal during 4 months of the year and illustrates some of the secretion patterns mentioned. Additional examples of LH secretion patterns are shown in Fig. 4.

Because baseline values were sometimes unde-

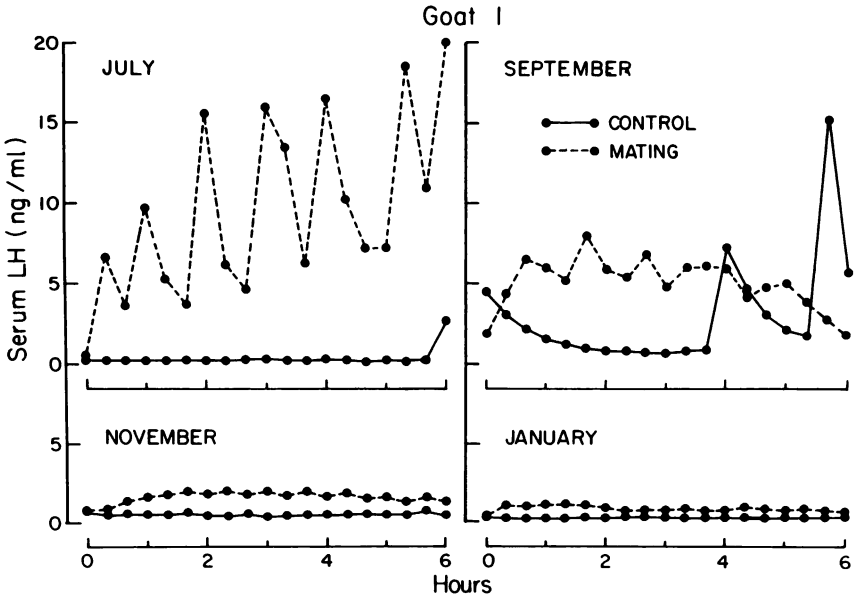

Fig. 3. Serum LH concentrations for a goat sampled every 20 minutes for 6 hours on control and mating days in July, September, November, and January.

tectable and in other instances could not be defined because of fusion of peaks, mean levels, baseline levels, and peak amplitude were not quantitated; peak frequency, however (the number of LH peaks/6 hours), was determined. Peak frequency and the number of animals showing LH peaks for control and mating days for each month are shown in Table 1. Peak frequency showed a seasonal pattern (month, $P < 0.01$) and was increased by mating (mating, $P < 0.05$). The mating effect varied with month (mating × month, $P < 0.01$) and was most obvious during June and July.

Relationship between LH, Testosterone, and Cortisol

Individual samples from two goats were assayed for testosterone and cortisol in addition to LH during the months of July (when mating markedly affects all 3 hormones), September (the month when LH and testosterone are both elevated), and January (when both LH and testosterone are approaching a seasonal low). Data from one animal was chosen to demonstrate secretion patterns of the three hormones in each of these months (Fig. 4). Both LH and testosterone were relatively low on control days in July and January. Cortisol levels fluctuated over the 6-hour periods. There were no obvious relationships among the levels of the three hormones. In September on the control day, four complete episodic releases of LH were observed and each was followed 20 to 40 minutes later by a rise in testosterone concentration. The secretion patterns for cortisol appeared to be independent of changes in LH or T. On mating days in July and September, LH-induced testosterone peaks were observed again. Although cortisol levels were elevated as a result of mating activity and fluctuated markedly, the pattern of secretion again appeared to be independent of the other two hormones. On the mating day in January, in spite of no measurable changes in LH over the 6-hour period, testosterone levels in goat 2 showed four peaks, and each was clearly associated with a simultaneous peak in cortisol. A similar observation was made on goat 3 (data not shown).

Because of the observation that testosterone and cortisol levels varied synchronously, testosterone and cortisol were determined on the mating days for the remaining goats in January, and for all four animals in March. The correlations between the two hormones are presented in Table 2. In January, cortisol and testosterone levels were significantly correlated ($P < 0.01$) in all animals. In March, the hormonal relationship remained in only two animals.

Discussion

In contrast to the ram, where seasonal (Barenton and Pelletier, 1983) and light-induced (Lincoln and Short, 1980; Howles et al, 1982) changes in testis

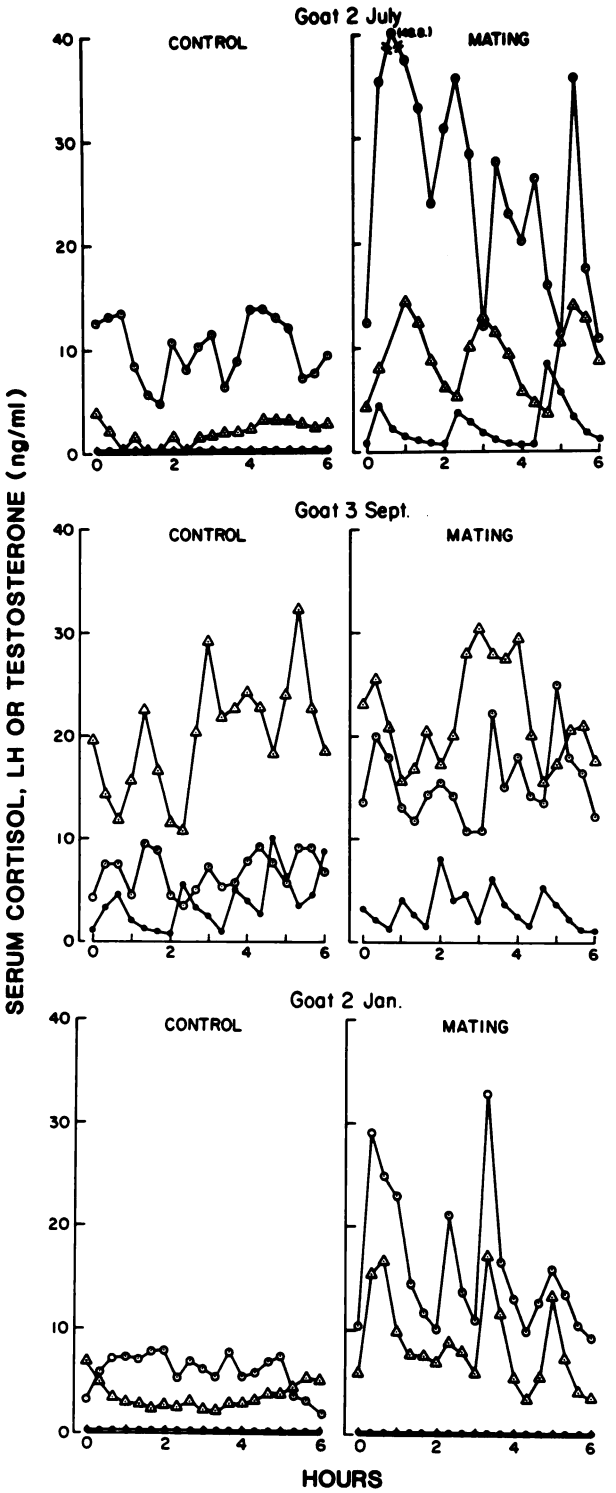

Fig. 4. Serum concentrations of cortisol (○), LH (●), and testosterone (△) for individual goats sampled every 20 minutes for 6 hours on control and mating days in July, September, and January.

size occur, the testis size in the the male pygmy goat appears to be relatively unaffected by season. The goats in the study also showed no obvious seasonal pattern in libido. Although Sanford et al (1977) reported increased mating performance as the breeding season advanced, other work (Dickson, 1981) indicates a lack of seasonal differences in sex drive. Perhaps in goats, as well as sheep, relatively low testosterone levels are required to bring about complete mating activity (D'Occhio and Brooks, 1982).

In spite of the existence of libido and the maintenance of testicular size throughout the year, the marked seasonal endocrine changes observed in these goats are clearly indicative of a seasonal breeder. In general, the seasonal changes in circulating levels of FSH, PRL, and testosterone are consistent with those observed in rams (Ravault, 1976; Dickson, 1981; Howland et al, 1983) and deer (Mirachi et al, 1978; Bubenik et al, 1982). With the exception of the late spring elevations in serum FSH and LH reported by Muduuli et al (1979), the present data agree with the seasonal changes previously reported for younger male pygmy goats.

The seasonal rise in LH levels observed in the present study occurred in September, somewhat later than the timing of this event in rams (Sanford et al, 1974a; Dickson, 1981; Howland et al, 1983). The observation that the seasonal rise in LH peaked when testosterone levels were approaching a maximum, coupled with the finding that testis size did not vary significantly with

TABLE 1. Mean Number of LH Peaks/6 Hours on Control and Mated Days in Four Pygmy Goat Bucks Throughout the Year

Month	Treatment	
	Control	Mated
June	0 (0)*	3.25 (4)
July	0 (0)	3.00 (4)
August	1.75 (4)	3.50 (4)
September	4.00 (4)	2.00 (3)
October	3.25 (3)	1.25 (2)
November	0.50 (1)	0 (0)
December	0 (0)	0 (0)
January	0 (0)	0 (0)
February	0 (0)	0.25 (1)
March	0 (0)	0.75 (1)
April	0 (0)	1.00 (2)
May	0 (0)	0.25 (1)
June	0.25 (1)	1.75 (3)

* Figures in brackets indicate the number of animals showing LH pulses.

TABLE 2. Correlation between Serum Concentrations of Cortisol and Testosterone on Mating Days in January and March

Goat No.	Correlation Coefficient	
	January	March
1	0.80*	0.70*
2	0.89*	0.45†
3	0.80*	0.19
4	0.71*	0.19

* $P < 0.01$.
† $P < 0.05$.

season, suggests that some aspects of the mechanism of seasonal changes in endocrine function of the testis may differ in sheep and goats. In rams, peak LH levels are associated with increases in testicular LH receptor concentration which, in combination with elevated LH levels, may explain in part the subsequent increase in testosterone synthetic activity by the testis (Barenton and Pelletier, 1983). In the pygmy goat, the time lag between the LH rise and the subsequent events leading to greater testosterone output by the testes appears to be abbreviated.

Considering the seasonal pattern of hormone secretion in the male pygmy goat, it might be expected that the peak of the breeding season for this breed of goat would coincide with, or immediately follow, the autumnal peak in testicular endocrine function. Although testosterone levels varied greatly with season, the male libido did not appear to be profoundly influenced. Surprisingly, observations on does maintained in the same barn revealed that estrous cycles did not begin until November and continued through late May (Kakusya et al, 1982); the relatively late and prolonged breeding season of the pygmy goat is not consistent with the limited period of high testosterone concentration in the males.

There was no obvious seasonal pattern in serum cortisol levels. This is consistent with observations made in white-tailed deer (Bubenik et al, 1975). The reason for the marked rise in control-day cortisol levels in May and June is not known. This was associated with a decline in libido and a lack of a mating effect on cortisol levels. The data suggest that some other factor(s) that were unrelated to the study were stressing the animals during the final months.

Mating and/or aggressive behavior associated with mating days had a profound effect on each of the hormones studied, except during periods when they were already seasonally elevated. This agrees with and extends the available data on rams, which indicate that LH and testosterone can be elevated by periods of intensive sexual activity (Sanford et al, 1974b; Moore et al, 1978; Yarney and Sanford, 1983). The increase in LH peak frequency on mating days during the summer months preceding the fall breeding season is similar to results observed in rams (Sanford et al, 1974b; Yarney and Sanford, 1983). Although mating increased FSH levels in January (Sanford et al, 1976), other observations between July and December revealed no significant effect of mating on this hormone (Sanford et al, 1977; Yarney and Sanford, 1983). Yarney and Sanford (1983) also reported no significant effect of mating on serum prolactin during July or October; in October, however, mounting without intromission significantly elevated prolactin levels.

In the present study, we cannot distinguish between the effects of sexual activity and the generally aggressive behavior and fighting that prevailed on mating days. Since the animals were placed in adjacent pens for ease of observation and bleeding, they had the opportunity to stand against the dividing fence and attempt to fight. Although no quantitative data was collected, it appeared that the bucks spent considerably more time engaging in aggressive activity than in any form of sexual activity. Although this behavior, and the presumed stress associated with it, probably is normal for goats and other seasonally breeding ungulates that attempt to gather and guard harems during the breeding season, it complicates the interpretation of the endocrine changes associated with mating. It is possible that the elevations in cortisol and prolactin noted on mating days were largely stress effects. Sexual activity also results in elevated cortisol levels in boars (Liptrap and Raeside, 1978) and stallions (Tamanini et al, 1983).

The observation of a relationship between cortisol and testosterone is intriguing but difficult to explain. Although LH-induced rises in testosterone were clearly evident when LH levels were measurable and episodic releases of LH occurred, the marked changes in testosterone on mating days in January were not related to any measurable changes in LH, but clearly were associated with coincidental changes in cortisol. Although there is no obvious explanation for this hormonal

relationship, it may provide a mechanism of elevating testosterone during periods of mating or aggression in the absence of the appropriate hypothalamic–pituitary response; perhaps, at other times of the year, changes in LH occur in response to mating-related stimuli.

In the boar, testosterone levels are elevated during either sexual or aggressive behavior, and this is correlated with an elevation in corticosteroids (Liptrap and Raeside, 1978). In this species, injected cortisol also elicits a rise in testosterone (Liptrap and Raeside, 1975). In bulls, however, stress-induced elevations in cortisol are associated with reduced testosterone secretion, and this effect may be due to direct suppression of Leydig cell steroidogenesis (Welsh and Johnson, 1981; Welsh et al, 1982). The possible relationships between glucocorticoids and testosterone in rams and males of other species during mating periods and the likelihood of species differences makes this problem worthy of additional study.

Acknowledgments

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