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Relation between progesterone concentrations during the early luteal phase and follicular dynamics in goats

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Abstract

We studied the relationship between progesterone (P_4) concentrations early in the estrus cycle and follicular dynamics in dairy goats. We used seven untreated goats (control group) and six progesterone treated goats (P group) with a controlled internal drug release device from Days 0 to 5 (Day 0: day of ovulation). We performed daily ultrasonograph during the interovulatory interval to determine ovarian change and took daily blood samples to determine serum estradiol 17β (E_2) and P_4 concentrations by RIA. We divided the control goats into 3- ($n = 4$) and 4-wave goats ($n = 3$), according to the number of follicular waves recorded during the ovulatory cycle. Mean progesterone concentrations between Days 1 and 5 were higher and mean estradiol concentrations between Days 3 and 5 were lower in 4-wave goats (P_4 : 3.8 ± 0.2 ng/ml; E_2 : 1.6 ± 0.2 pg/ml) than in 3-wave goats (P_4 : 2.0 ± 0.5 ng/ml, $P \leq 0.05$; E_2 : 4.4 ± 0.9 pg/ml, $P \leq 0.05$). Wave 2 emerged earlier in 4-wave (Day 4.2 ± 0.3) than in 3-wave goats (Day 7.3 ± 0.3 , $P \leq 0.05$). Three out of six of the progesterone-treated goats had short cycles (mean 8.0 ± 0.0 days) and ovulated from Wave 1. The other three goats had shorter cycles (mean 18.3 ± 0.3 days) than the control group (20.0 ± 0.2 days; $P \leq 0.05$), although they were within the normal range of control cycles (shortened cycles). In the three treated goats with shortened cycles (two with four waves, one with three waves), mean progesterone concentrations between Days 1 and 5 were higher (4.7 ± 0.6 ng/ml) than in the 3-wave control goats. In these goats, Wave 2 emerged at Day 4.3 ± 0.3 , similar to the time observed in 4-wave goats but earlier ($P \leq 0.05$) than in 3-wave control goats. Overall results confirm a relationship between the progesterone levels and the follicular wave turnover during the early luteal phase in the goat. Higher progesterone concentrations may accelerate follicular turnover probably by an early decline of the negative feedback action of the largest follicle of Wave 1. This is followed by an early emergence of Wave 2. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

By using transrectal ultrasonography, researchers have demonstrated that ovarian follicular development occurs in wave-like patterns in cattle and other ruminants [1]. Researchers agree that, in the cow, most cycles present two or three follicular waves. Although it has been demonstrated that each follicular wave is preceded by a rise in serum follicle-stimulating hormone (FSH) concentrations, the exact mechanism for the existence of a 2- and 3-wave pattern in cows is unknown. However, Sirois and Fortune [2] found that luteal levels of progesterone promote both the turnover of the dominant follicle and a regular succession of follicular waves in cattle. Thereafter, more precise studies on the role of progesterone were performed in cattle and sheep [3,4]. Exposure to high levels of exogenous progesterone during the early luteal phase suppressed the dominant follicle of Wave 1 in the cow [3] and the ewe [4] and accelerated the emergence of the next wave. In contrast, when subluteal progesterone levels were induced, the growth of the dominant follicle of Wave 1 was prolonged and a delay of the emergence of the next wave was evident in both species [3,5].

Until today, few studies have used ovarian ultrasonography in goats [6–8]. These authors agree upon the existence of a wave-like pattern of follicular growth in the goat; nevertheless, these studies reported a large variation in the number of follicular waves (2–5) during the ovulatory cycle. Differences could be due to numerous causes (i.e. breed, season, body condition) but in one report [6], we showed that mean serum progesterone concentrations were higher during the early phase of the cycle in the goats with more follicular waves (four waves versus two–three waves).

We focused the present study on the follicular changes during the interovulatory cycle in dairy goats. We studied the relationship between peripheral serum steroid concentrations and follicular wave turnover in cycling goats, and tested the hypothesis that high progesterone levels during the early luteal phase affect the activity of the largest follicle of Wave 1 and advances the emergence of the next wave.

2. Materials and methods

2.1. Animals and treatment

We used 13 multiparous Saanen X Anglo Nubian crossbreed dairy goats during the breeding season (April–August) at the experimental laboratory of the Department of Physiology, Montevideo, Uruguay (35° SL). The does weighed 48.8 ± 2.0 kg (mean \pm S.E.M.), and had a mean body condition score of 3.0 ± 0.1 (scale: 0–5). During the experiment, the animals were fed alfalfa hay and pellets (1500 and 700 g/goat/day, respectively) and water was available ad libitum. We housed the goats outdoors in a sheltered pen (30 m \times 30 m), and we used indoor box stalls (3 m \times 3 m) for ultrasonic examinations.

We synchronized estrous cycles with two injections of a PGF_{2 α} analogue (160 μ g, im, Glandinex, Universal Lab, Montevideo, Uruguay) 9 days apart. After synchronizing the cycle, we assigned the goats to a control group (control group, $n = 7$) or a progesterone-treated group (P group, $n = 6$). In the P group, progesterone was administered for 5 days

using a controlled internal drug release device (CIDR-G, Eazi Breed, InterAg, New Zealand) containing 0.3 g of progesterone placed the day ovulation (Day 0) was detected by ultrasonography.

2.2. Interestrous intervals

We checked estrous behavior with a vasectomized buck, for 45 min twice a day, throughout the experiment. We defined estrus by the period when we observed the doe standing to be mounted by the buck. We classified the interestrous interval as of “short” (<12 days) or of “normal” duration (range: 17.5–22 days).

2.3. Ultrasonic evaluations

We obtained ovarian images with a B-mode machine (Aloka 210, Tokyo, Japan) equipped with a 5 MHz linear array transducer. We fastened a slightly arched plastic open tube (diameter, 25 mm; length, 40 cm) to the transducer with tape so that the probe could be manipulated externally into the rectum [4]. We carried out daily ultrasonic examinations with the same operator between 16:00 and 19:00 h for 6 weeks prior to the start of the study as training and as a way to facilitate goat management. During the examination, we restrained the goats in a standing position in a wooden chute designed for that purpose. We removed fecal pellets by hand and introduced carboxymethylcellulose gel (50 ml) into the rectum [4] with a syringe. The procedure to locate the ovaries was the same as described by Ginther and Kot [7].

We recorded the diameter, positions and characteristics of the CL and the antral follicles ≥ 3 mm in diameter. The location of follicles relative to each other and to the CL was sketched on paper. After registering the locations and diameters, we compared the sketch with those of the previous days. We also recorded the examination on videotapes, using one tape per goat (Sony, Tokyo, Japan), for further analysis of data.

2.4. Follicle data analysis

When we first detected a follicle at 4 mm, we presumed that the follicle had been 3 mm on the previous day. The day of emergence of a follicle was the day on which a follicle was 3 mm in diameter, followed by an increase in diameter to ≥ 4 on the following day. The term wave was defined as a group of follicles that gave origin to one or more follicles ≥ 5 mm in diameter. The day on which the largest follicle of a wave emerged was considered to be the day on which that wave emerged, and more than 1 day was allowed for all the follicles of a wave to emerge [7]. We defined the interwave as the time between the emergence of two consecutive waves. Ovulation was detected ultrasonographically by the collapse of a large follicle.

2.5. Hormone analysis

We collected daily blood samples for hormone determinations by jugular venipuncture, using vacutainer tubes from 1 day before synchronized estrus. We allowed samples to clot

at room temperature and centrifuged them within 2 h after collection. Serum was stored at -20°C until hormone determination.

We determined concentrations of progesterone by a direct solid-phase RIA (DPC, Diagnostic Products Co., Los Angeles, CA, USA), which was previously described [9]. The detection limit of the assay was 0.1 ng/ml. The intra- and inter-assay coefficients of variation were 7 and 9%, respectively. The luteal phase was defined as the interval between the day of ovulation and the day that progesterone concentrations declined below 1.0 ng/ml.

We determined estradiol 17β concentrations in samples taken on Days 0–10 in duplicate using previously validated ^{125}I radioimmunoassay kits (Diagnostic Products Co, Los Angeles, CA, USA) [10]. For the assay, we extracted 250- μl aliquants of serum with 2.5 ml diethyl ether; the volume of extracted serum used was 200 μl /tube. The standard curve was also extracted. The E_2 antiserum cross-reacted with estriol at 0.24%, with androstenedione at 0.004% and at undetectable levels with progesterone and testosterone. The detection limit of the assay was 0.6 pg/ml. The intra-assay coefficients of variation were 24% for a concentration of 1.5 pg/ml and 15% for a concentration of 13.5 pg/ml. The inter-assay coefficients of variation were 25% (1.5 pg/ml), and 16% (13.5 pg/ml).

2.6. Statistical analysis

We compared the interestrous and the interovulatory intervals, the duration of the luteal phase, the interwave intervals and the characteristics of the largest follicles by ANOVA. We analyzed the mean daily concentrations of progesterone and estradiol by the general linear model (GLM) procedure of the Statistical Analysis System to establish whether there was a group and day effect and group \times day interaction [11]. The data are presented as means \pm S.E.M., and differences were considered to be significant when $P < 0.05$.

3. Results

3.1. Control goats

We identified three follicular waves in four control goats and four follicular waves in the other three goats. Thereafter control goats were classified as 3- and 4-wave goats. Three- and four-wave goats did not differ in duration of the interestrous interval (20.4 ± 0.3 and 20.3 ± 0.8 days, respectively), interovulatory interval (20.0 ± 0.0 and 19.9 ± 0.6 days, respectively) nor in the duration of the luteal phase (18.3 ± 0.6 and 17.3 ± 0.9 days, respectively).

The mean day of emergence of the largest follicle of Wave 1 and the mean maximum diameter attained by this follicle did not differ between 3- and 4-wave goats. However, in 4-wave goats, the largest follicle of Wave 1 tended ($P = 0.07$) to attain its maximum size earlier (Table 1).

The largest follicle of Wave 2 emerged earlier (Table 1) and also attained its maximum diameter earlier in 4-wave goats than 3-wave goats (Days 8.9 ± 0.6 versus 11.5 ± 0.3 ; $P \leq 0.01$), but the maximum diameter was similar (6.2 ± 0.6 versus 6.4 ± 0.5 mm;

Table 1

Relation of progesterone concentrations (mean \pm S.E.M.) during the early luteal phase and the largest follicle of Wave 1 and its influence on subsequent follicular waves in 3- and 4-wave control goats compared with progesterone treated goats that showed shortened cycles

	Control		Progesterone treated shortened cycles ($n = 3$)
	3-waves ($n = 4$)	4-waves ($n = 3$)	
Mean progesterone (ng/ml)			
Days 1–5	2.2 \pm 1.1 a	4.1 \pm 0.7 b	5.2 \pm 0.8 b
Days 6–10	5.8 \pm 0.5	7.9 \pm 0.7	5.3 \pm 0.5
Wave 1			
Day of emergence	0.0 \pm 0.4	–0.3 \pm 0.3	0.0 \pm 0.0
Day of maximum diameter	6.3 \pm 0.3 a	5.3 \pm 0.3 ab	4.0 \pm 0.0 b
Inter-wave interval (between Wave 1 and 2)	7.3 \pm 0.5 a	4.6 \pm 0.3 b	4.3 \pm 0.3 b
Wave 2			
Day of emergence	7.3 \pm 0.3 a	4.2 \pm 0.3 b	4.3 \pm 0.3 b
Day of maximum diameter	11.5 \pm 0.3 a	8.9 \pm 0.6 b	9.0 \pm 1.0 b
Inter-wave interval (between Wave 2 and 3)	6.0 \pm 0.4	5.2 \pm 0.3	4.3 \pm 0.3
Wave 3			
Day of emergence	13.3 \pm 0.3 a	9.5 \pm 0.3 b	8.7 \pm 0.3 b

Values with different letters (a,b) differ ($P \leq 0.05$).

respectively). The interwave interval between Waves 1 and 2 was shorter in 4-wave than 3-wave control goats. The day of emergence of the ovulatory wave occurred 1 day earlier in 3-wave goats but did not differ statistically (Days 13.3 \pm 0.3 and 14.2 \pm 0.9, for 3- and 4-wave goats, respectively).

In 4-wave control goats, progesterone concentrations reached values over 1.0 ng/ml earlier than in 3-wave goats (Days 1.0 \pm 0.0 and 2.8 \pm 0.5; respectively, $P \leq 0.05$) and they were also higher from Days 1 until 5 (mean: 4.1 \pm 0.7 and 2.2 \pm 1.1 ng/ml, respectively, $P \leq 0.05$) (Table 1).

Mean serum estradiol 17 β concentrations between Days 3 and 5 were higher in 3-wave than 4-wave control goats (4.4 \pm 0.9 and 1.6 \pm 0.2 pg/ml, respectively, $P < 0.05$) (Fig. 1).

3.2. Progesterone-treated goats

Serum progesterone concentrations increased soon after placing CIDR (Day 1: 6.0 \pm 2.1 ng/ml). At Day 2, progesterone concentrations were higher (5.4 \pm 0.4 ng/ml) than in 3- and 4-wave control goats (1.0 \pm 0.2 and 2.2 \pm 0.2 ng/ml, $P \leq 0.05$; respectively) and they remained high until CIDR withdrawal (Day 5: 5.1 \pm 0.8 ng/ml). Thereafter, treated goats showed two different responses. In three goats, progesterone concentration fell rapidly to basal levels, followed by estrus and ovulation (short cycles). In the other three treated goats, progesterone concentrations were similar to those of the control goats but fell to values less than 1.0 ng/ml earlier (Day 15.7 \pm 0.3 versus Days 18.3 \pm 0.7 and 17.7 \pm 0.8; treated goats versus 3- and 4-wave control goats, respectively $P \leq 0.05$). The individual interovulatory intervals of these goats were within the normal range (17.5–22 days) but the mean interovulatory interval was shorter than in the control

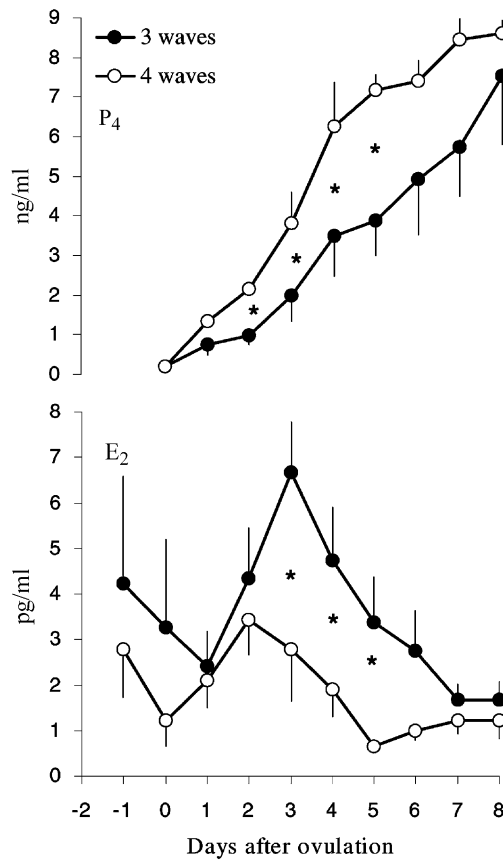


Fig. 1. Mean serum progesterone (P₄) and estradiol (E₂) concentrations in 3- ($n = 4$) and 4-wave ($n = 3$) untreated goats during the early luteal phase. Days labeled with an asterisk (*) indicate differences ($P \leq 0.05$) among groups.

group (18.3 ± 0.3 days versus 20.0 ± 0.2 days, respectively, $P \leq 0.01$). Hence, this response of treated goats was classified as “shortened” cycles.

Serum estradiol concentrations did not differ among treated goats until Day 5 (day of CIDR withdrawal), but they increased thereafter in the three goats that developed short cycles, in association with the follicular phase. In the other three treated goats, mean estradiol concentrations remained low and did not differ from the control goats. Two of these goats showed four follicular waves and the other one showed three follicular waves during the intervovulatory interval. In the three treated goats with short cycles, the ovulatory follicles were derived from Wave 1.

4. Discussion

Control goats had interovulatory and intervovulatory intervals similar to those reported in previous studies [12]. On the other hand, progesterone treatment during the early luteal

phase affected the length of these intervals in ways that are similar to those described for the cow [13,14] and the ewe [15]. These findings were reported in a preliminary abstract [16].

In this study, we focused on follicular dynamics during the early luteal phase. Our results confirm the existence of a wave-like pattern of follicular development during the ovulatory cycle of the goat [6–8]. In the present study, both control and progesterone-treated goats with shortened cycles showed three or four follicular waves. The length of interovulatory interval in cattle has been associated with the number of follicular waves, and a later luteal regression has been observed in relation with more follicular waves [17]. In this report, progesterone levels were not measured, and these authors used the ultrasonic characteristics of the CL to define the length of the luteal phase. In another report [18], no differences in cycle length were found among heifers with different numbers of follicular waves. In the few ultrasonic studies conducted in goats, no differences in interovulatory intervals have been reported in does with different numbers of follicular waves [6,7]. Likewise, in the few animals in the present study, the duration of the luteal phase and/or the interovulatory interval were similar for the 3- and 4-wave goats.

The results show a relationship between higher progesterone levels during the early luteal phase and an acceleration of the follicular turnover. This is in agreement with pharmacological studies performed in the cow [3] and the ewe [4], and it confirms the observations of de Castro et al. [6] after scanning cycling goats. When the progesterone concentrations increased early in untreated goats, the emergence of the Wave 2 was advanced. Thereafter, the emergence of subsequent waves was also advanced and these goats showed a 4-wave pattern during their ovulatory cycle. In contrast, in the goats that developed three waves, the interwave interval between Waves 1 and 2 was more prolonged and Waves 2 and 3 emerged later than in 4-wave goats (Table 1).

In treated goats, in which exogenous progesterone treatment started soon after ovulation, the follicular turnover was stimulated. The high progesterone levels induced by the insertion of a CIDR affected the growth of the largest follicle of Wave 1 and the emergence of Wave 2 was advanced in a way similar to that observed in 4-wave control goats. A similar response was observed in heifers where higher progesterone levels shortened the interval to the emergence of the following wave [3].

In addition to the higher progesterone concentrations observed on Day 2 in 4-wave control goats compared with the 3-wave control goats, we found lower estradiol concentrations in these goats 1 day later. In ewes during the early luteal phase, the development of waves of follicular growth is associated with an increased secretion of estradiol associated with the period of high LH pulse frequency [19]. As has been shown by Haugher et al. [20], high progesterone levels suppressed pituitary LH pulse frequency; this could explain the lowered estradiol concentrations in the present study. Alternatively, the early progesterone exposure could have reduced the capacity of the follicle to secrete estradiol by directly inhibiting the aromatase enzyme complex, as was demonstrated in anestrus ewes [21].

Follicle-stimulating hormone (FSH) surges necessarily precede the emergence of a follicular wave in heifers [22,23], and a similar association of both events has been reported in ewes [24–26], but we did not measure FSH levels in the present study. According to Baird et al. [27], FSH secretion was not affected directly by progesterone but was regulated

by estradiol and inhibin, which was produced mainly by the largest follicles that developed during the cycle. In the treated goats and 4-wave control goats of this study, higher progesterone levels early in the cycle possibly suppressed pituitary LH pulses and/or had a direct inhibition on follicular secretions by the largest follicle of Wave 1 earlier than in 3-wave control goats. Therefore, this premature inhibition on follicular activity could have suppressed the negative feedback on pituitary FSH release and a new FSH surge could have advanced the emergence of a new follicular wave. This mechanism could explain the advancement of Wave 2 in both treated goats and in 4-wave untreated goats.

In conclusion, the results of the present study support the idea that progesterone may be a significant differentiating factor for 3- or 4-wave cycling goats. High progesterone concentrations early in the early luteal phase may lead to an increase in follicular turnover as the emergence of the next wave is accelerated.

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