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Follicular dynamics in Serrana goats

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Abstract

Twenty-two Serrana goats were studied through two successive estrous cycles in order to characterize their follicular dynamics during the breeding season. The ovaries of the goats were scanned daily by real-time ultrasonography and all follicles ≥3 mm were measured and classified. The data were classified by the number of follicular waves per goat to test the hypothesis that temporal and morphological differences between the last follicular wave of an ovary, irrespective of ovulation, will affect the selection of the next ovulatory wave.

The mean interovulatory interval was 20.7 ± 1.0 days (mean ± S.D.). Three to five waves per estrous cycle were observed and 61.3% (19/31) of cycles had four waves. In estrous cycles with four waves, the day of onset of the first, second, third and fourth wave was 1.4 ± 1.0, 6.9 ± 1.4, 11.6 ± 1.8 and 16.8 ± 1.6, respectively. No differences ($P > 0.05$) were found between the day of onset of the first and second waves for estrous cycles with three, four or five waves. However, the day of onset of the third and fourth waves occurred later when the number of waves per estrous cycle increased ($P < 0.001$). The duration of the interwave interval (time between the day of onset of two consecutive waves) was longer when the second wave was ovulatory. The length of the growth phase (2.4 ± 0.9 days) and size (5.9 ± 0.7 mm) of the dominant follicle in the second wave were lower ($P < 0.01$) than for the first wave (3.3 ± 1.2 days and 6.6 ± 0.9 mm, respectively) and the fifth wave (4.1 ± 1.2 days and 7.5 ± 1.0 mm, respectively). Within pairs of ovaries, the onset of the last wave occurred later ($P < 0.05$) and was less variable in ovulatory ovaries (day 16.8 ± 1.4, $n = 20$) than in anovulatory ovaries (day 15.1 ± 3.7, $n = 20$). The length of the growing phase was longer ($P < 0.001$) in the last waves of ovulatory ovaries (3.1 ± 0.9 days) than in the last waves of anovulatory ovaries (1.7 ± 0.8 days). These results support the hypothesis that the day of onset of the ovulatory wave is related to or, at least, conditioned by the luteolysis and the decrease in plasma progesterone.

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In summary, the estrous cycle of Serrana goats is characterized by sequential follicular wave growth with a great variability in their onset and duration, with the exception of the ovulatory wave. The temporal and morphological differences observed in the last wave of estrous cycle provide strong evidence for the role of progesterone in their regulation.

Keywords: Estrous cycle; Follicular dynamics; Ovary; Goat; Ultrasonography

1. Introduction

Follicular dynamics during the estrous cycle of the goat were first reported by Ginther and Kot (1994) using real-time ultrasonography (UTR). These authors frequently found four follicular waves in the estrous cycle and suggested that follicular dominance occurred in first and last waves. These results have been confirmed by other reports (de Castro et al., 1998, 1999; González de Bulnes et al., 1999; Padilla and Holtz, 2000), and are similar to the follicular dynamics observed in other ruminant species (see reviews of Adams (1999), Ireland et al. (2000) and Mihm et al. (2002)).

The occurrence of reduced, or lack, of follicular dominance in some waves in the middle of the estrous cycle of polyovular species (sheep and goats) has been reported by some authors (Schrick et al., 1993; Orita et al., 2000), but there is no agreement on this point (Bartlewski et al., 1999; Gibbons et al., 1999; Evans et al., 2000). In cows, the pattern of hormonal and follicular dynamic of waves with co-dominant follicles or one dominant follicle has some differences (Kulick et al., 2001) to small ruminants.

Recent studies linking the morphological and functional characteristics of ovarian structures have provided an understanding of the relationships between progesterone (P4), estradiol, FSH or inhibin to goat ovarian dynamics (Gonzalez-Valle et al., 1998; de Castro et al., 1999; Schwarz and Wierzchos, 2000; Menchaca and Rubianes, 2002; Medan et al., 2003).

Rubianes and Menchaca (2003) suggested that when ovulation is induced by luteolysis the ovulatory follicle could be dominant follicle of an existing wave in either the growing or static phase. The ovulatory follicle was present at the time of the induced luteolysis in a significant proportion of the goats in the study of Gonzalez-Bulnes et al. (2005).

Studies of follicular dynamics in the natural estrous cycle of goats (Ginther and Kot, 1994; de Castro et al., 1999; Medan et al., 2003) show that there are no significant differences between the last two waves of the cycle or between these waves and the previous ones. However, these studies show a great variability in the number of follicular waves and it may be important to characterize them in relation to the number of waves present in the estrous cycle. The data of these studies were analyzed by combining the waves of each ovary, since both ovaries receive the same hypophyseal-pituitary signal, although the asymmetry of the follicular dynamics between right and left ovary has been recognized (see review of Driancourt (2001)).

This asymmetry between ovaries could be partially related to some local effects, which were recently reviewed by Rubianes and Menchaca (2003). Temporal analysis of the last follicular wave of each ovary within a goat could reveal some differences between these last two waves.

We hypothesised that there are some differences between the last two waves of the estrous cycle or between the beginning of the last wave of the ovulatory and anovulatory members of a pair of ovaries that reflect the selection mechanisms of the ovulatory wave.

The aims of the present study with Serrana goats were to (1) characterize follicular dynamics during the estrous cycle according to the number of waves per goat during the breeding season and (2) test the hypothesis that there are temporal and morphological differences between the ovulatory and anovulatory ovary of a pair of ovaries in terms of their last wave, that could contribute to understand the mechanisms of ovulatory wave selection.

2. Materials and methods

2.1. Animals

The study was carried out at the experimental farm of University of Trás-os-Montes e Alto Douro (UTAD), located in Vila Real (latitude 41°19′N; altitude 479 m).

Twenty-two Serrana goats, 13 nulliparous and 9 multiparous, weighing 18.5–52.0 kg were used. The goats underwent a 6 month adaptation period to the experimental conditions. The Serrana goat is a local Portuguese breed found in the mountain regions of the north and centre of the country. The animals are predominantly kept for milk production. A seasonal anoestrous period, from January to May, has been observed in this breed (Mascarenhas et al., 1995).

The experiment was conducted from September to November (breeding season). Two sequential estrous cycles were studied: the first one was induced and the following two were natural. Ovarian activity and estrous cycle phase were previously confirmed by twice a week determination of plasma progesterone levels, over a period of 4 weeks.

Ovulation was synchronized with two intramuscular administrations of 50 μg cloprostenol (Estrumate®, Schering-Plough Animal Health, Germany), 10 days apart. Estrous detection was performed using two vasectomized bucks with marker harnesses. Checking of mounting marks and estrous signals were performed continuously from 20 to 96 h after the second prostaglandin administration and during the expected estrous period.

2.2. Blood samples and hormonal assay

To identify the phase of the estrous cycle, jugular blood samples were collected twice weekly in heparinized tubes, throughout the experimental period. Plasma was separated by centrifugation and frozen (−60 °C) until progesterone assay by RIA (Kubasik et al., 1984).

Just after the first mount observation (which was designated as the onset of estrous), each goat was isolated from the group and blood samples were collected every 4 h for 24 h. The plasma was stored, as previously described, until LH assay by RIA (Pelletier et al., 1968).

All ovulations were confirmed by three methods: identification of the LH preovulatory peak, observation of the loss of preovulatory follicles (by UTR) and observation of a CL after the third day of the estrous cycle (by UTR). Ovulation time was identified by LH quantification and UTR scanning, performed every 4 h, during the estrous period.

2.3. Ultrasound scanning

The equipment (Aloka SSD 500 with probe model UST-660-7.5) and techniques used for transrectal ultrasound scanning of ovaries and measurement of the follicles have been described previously (Simões et al., 2005).

UTR scanning of both ovaries was performed every 4 h, from 20 to 44 h after the onset of each estrous, to detect the loss of the preovulatory follicle and the occurrence of ovulation.

Thereafter, UTR was performed daily for two complete estrous cycles. All sonograms were identified according to the ovary side and recorded with a digital video camcorder. The ovulations in the third estrous cycle were confirmed by counting the corpora lutea present between days 6 and 8 following ovulation.

2.4. Counting and classification of follicles and follicular waves

Tertiary follicles ≥2 mm diameter with spherical or oval conformation and smooth walls were identified by UTR and measured later. The relative topography of follicles was not considered.

The day of ovulation (D0 of the estrous cycle) was defined by the loss of follicles ≥5 mm followed by the development of a CL.

The following terminology was used:

- *Follicular wave*: Identified by the decrease in number of small follicles and the increase in diameter of at least one follicle which then regressed or ovulated.
- *Onset of follicular wave*: First observation of at least one follicle ≥3 mm diameter, followed by a growing follicular wave resulting in a follicle with a minimal diameter of 5 mm in the following 3 day period.
- *Day of maximum follicular diameter*: The first day in each wave when the dominant follicle reached its maximum diameter (greater than 5 mm);
- *End of follicular wave*: The day when the number of follicles <3 mm increased and the number of follicles ≥3 mm decreased by the same proportion.
- *Duration of wave*: Interval between the onset and the end of a follicular wave.
- *Interwave interval*: Interval between the onsets of a follicular wave and the subsequent follicular wave.

The last wave for each ovary was classified as ovulatory or not ovulatory (anovulatory), as appropriate. Follicular waves whose dominant follicle(s) had started growing during the previous estrous cycle were not considered. Similarly, the waves completed in the following estrous cycle were ignored.

The number of follicular waves per ovary, the onset and the end of each wave and the day when the dominant follicle reached maximum diameter were quantified for each estrous cycle.

The follicular waves of both ovaries within a goat were combined. Two waves of different ovaries within a pair were considered to be simultaneous when at least three-fourths of the duration of one wave took place at the same time as the other wave. When that occurred, the wave characterized for analysis was selected by the following criteria which were applied in decreasing order: (1) the dominant follicle persisted longer, (2) the wave had a greater duration, (3) the dominant follicle was larger, and (4) the day of wave onset was earlier. The last wave was the ovulatory wave. When both ovaries within a pair had ovulatory waves, only the wave with largest duration was considered.

2.5. Statistical analysis

The number and frequency of follicular waves, their relationship with the interovulatory interval and with the number of corpora lutea (CL) and the characterization of follicular waves were analysed for each goat.

Comparisons of the last waves of the anovulatory and ovulatory ovaries within a pair were analysed independently by goat.

Frequencies were compared by the χ^2 test. The comparison of mean values was done by ANOVA, and the Bonferroni/Dunn test. Simple linear regressions were carried out to compare data.

The statistical analyses were performed using Statview® 4.53 software (Abacus Concepts, Inc., SAS, 1999). Quantitative data are represented as mean ± S.D.

3. Results

The plasma progesterone profiles showed that all the goats (22/22) were cyclic at the beginning of the prostaglandin treatment.

In 15 goats, the preovulatory LH peak and ovulation time were identified in two consecutive estrous cycles; in seven goats, only the first estrous cycle was observed, because the subsequent LH peaks and/or ovulation time were not accurately detected in six of them and one goat died. Consequently, a total of 37 complete estrous cycles (22 induced cycles and 15 natural cycles) were observed. All the data were recorded for 91.9% (68/74) of the ovaries in these cycles. Data on the remaining ovaries were eliminated due to one of the following reasons: (a) difficulties in follicular identification by UTR on two or more successive days, (b) persistence of a dominant follicle through the whole estrous cycle, or (c) continuous presence of different sized follicles during at least two-thirds of the estrous cycle that made follicular wave identification difficult. All of these six anovulatory ovaries occurred in different goats.

The wave combination of both ovaries was performed in 31 estrous cycles.

All the preovulatory follicles originated from the last follicular wave.

3.1. Interovulatory interval and number of follicular waves

The mean inter-estrous ($n = 37$) and interovulatory ($n = 32$) intervals were similar (20.6 ± 1.0 days versus 20.7 ± 1.0 days; $P > 0.05$). In five estrous cycles, ovulation occurred from 20 to 44 h after the onset of estrous, but it was not possible to detect the precise time of ovulation. These intervals were not dependent ($P > 0.05$) on the type of estrous (induced versus natural).

The inter-estrous interval tended to be longer ($P = 0.06$) in multiparous (21.0 ± 0.7 days, $n = 14$) than in nulliparous (20.4 ± 1.1 days, $n = 23$) goats. Similarly, the interovulatory interval for multiparous goats (21.2 ± 0.8 days, $n = 12$) was longer than that for nulliparous goats (20.4 ± 1.1 days, $n = 20$; $P < 0.05$).

The mean number of follicular waves per estrous cycle ($n = 31$) was 4.1 ± 0.6, varying between three and five waves per cycle. The most common number of follicular waves, occurring in 61.3% (19/31) of the estrous cycles, was four (Fig. 1).

The parity, type of estrous, interovulatory interval, number of CL and time of onset of first follicular wave had no significant effect ($P > 0.05$) on the number of follicular waves per estrous cycle.

Fig. 2 shows a schematic example of the follicular dynamics with the wave combination of both ovaries of a goat during a natural estrous cycle.

3.2. Characterization of follicular waves

The duration of the first follicular wave (7.6 ± 1.8 days) was longer ($P < 0.001$) than for all other waves (Fig. 3) and the fourth wave (4.4 ± 1.3 days) was shorter ($P < 0.001$) than the second

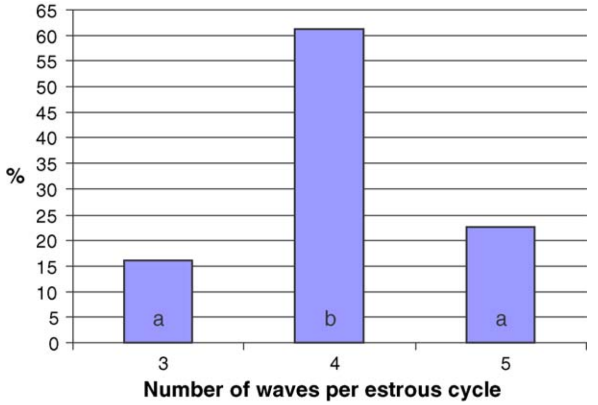

Fig. 1. Distribution of the number of follicular waves per estrous cycle in goats. Different letters within columns (a vs. b) show that the difference was significant ($P < 0.001$).

wave (5.6 ± 1.5 days) and the third wave (5.4 ± 1.3 days). The duration of the fifth wave was 4.6 ± 1.1 days.

When only the anovulatory waves were analysed, the duration of the first wave (7.6 ± 1.8 days) was longer ($P < 0.001$) than the second (5.6 ± 1.5 days), third (5.3 ± 1.4 days) and fourth

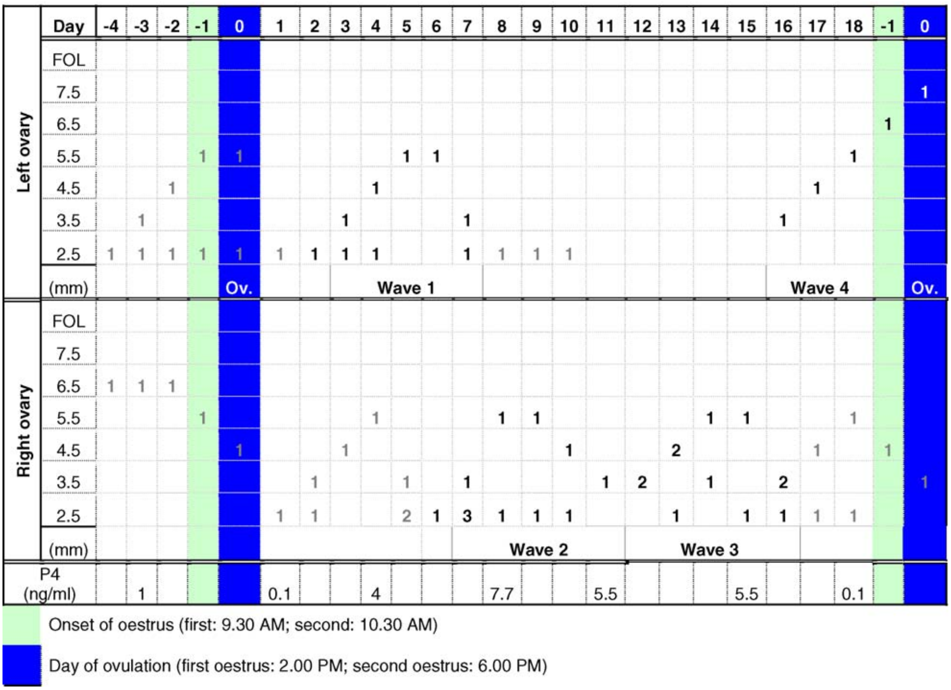

Fig. 2. Follicular dynamics of a goat through a natural estrous cycle. The cells show the number of follicles by size category for each day of the estrous cycle (ovulations occurred in the left ovary in both cycles). FOL: follicle diameter (mm).

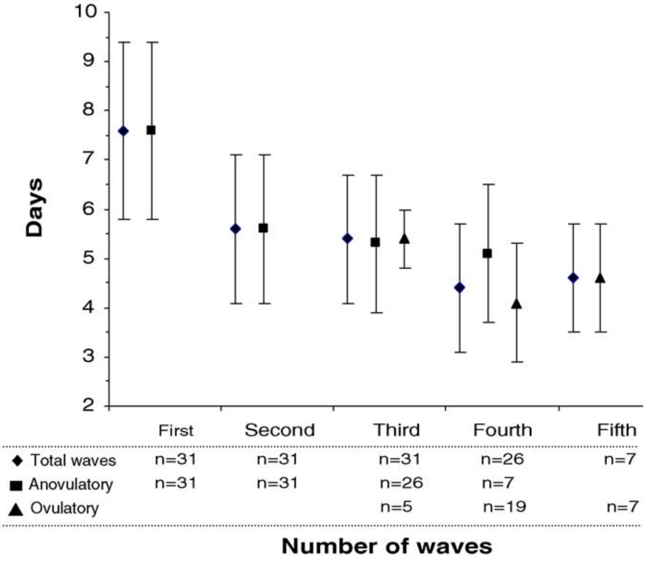

Fig. 3. Average length of follicular waves during the estrous cycle of goats. Data show means with bars for S.D.

(5.1 ± 1.3 days) waves. No differences were found ($P > 0.05$) between the length of the ovulatory wave in goats with three (5.4 ± 0.6 days), four (4.1 ± 1.2 days) and five (4.6 ± 1.2 days) waves per estrous cycle.

The total number of waves per estrous cycle did not affect ($P > 0.05$) the length of the first wave. This wave was always longer than the others.

The onset, the day of maximum follicular diameter and end of waves were, respectively, 1.0 ± 1.2, 4.4 ± 2.1 and 9.6 ± 1.8 days for the first wave and 7.6 ± 0.9, 9.8 ± 1.3 and 13.8 ± 2.2 days for the second wave. No differences were found ($P > 0.05$) in goats with three, four or five waves per cycle. The onset of each follicular wave, the day of maximum follicular diameter, and the last day of third or fourth waves were inversely related to the number of waves per ovary ($P < 0.001$; Table 1).

The first interwave interval was 5.6 ± 0.3 days ($n = 31$) and not significantly different ($P > 0.05$) between estrous cycles with three (6.6 ± 1.1, $n = 5$), four (5.6 ± 1.5, $n = 19$) or five (5.0 ± 2.1, $n = 7$) waves. The second interwave was longer ($P < 0.001$) in estrous cycles with three waves (7.2 ± 1.6 days, $n = 5$) than in estrous cycles with four (4.6 ± 1.3 days, $n = 19$) and five (3.1 ± 1.5 days, $n = 7$) waves. The third interwave interval was longer ($P < 0.01$) in estrous cycles with four waves (5.2 ± 1.4 days, $n = 19$) than in estrous cycles with five (3.7 ± 1.5 days, $n = 7$) waves. The duration of the fourth interwave was 3.7 ± 1.1 days ($n = 7$).

3.3. Growth and regression phases of the dominant follicle

The maximum follicle size in the fifth (7.5 ± 1.0 mm, $n = 7$) and fourth (6.9 ± 1.1 mm, $n = 26$) follicular waves was greater ($P < 0.001$) than in the third (6.0 ± 1.0 mm, $n = 31$) and second (5.9 ± 0.7 mm, $n = 31$) waves. The maximum size of dominant follicle in first wave (6.6 ± 0.9 mm, $n = 31$) was also larger ($P < 0.001$) than in the second wave.

Table 1
Time of onset, end and duration of follicular waves, and of maximum follicle diameter, in goats

No. of waves per cycle	Wave	Onset of wave (day)	First day of maximum follicular diameter	End of wave (day)	Length of wave (day)
Three ($n = 5$)	First	1.0 ± 1.2 a	4.4 ± 2.1 a	9.6 ± 1.8 a	8.6 ± 1.1 a
	Second	7.6 ± 0.9 a	9.8 ± 1.3 a	13.8 ± 2.2 a	6.2 ± 1.9 a
	Third	14.8 ± 1.3 a	19.8 ± 1.1 a	20.2 ± 0.8 a	5.4 ± 0.5 a
Four ($n = 19$)	First	1.4 ± 1.0 a	4.5 ± 1.2 a	8.4 ± 1.8 a	7.0 ± 1.9 a
	Second	6.9 ± 1.4 a	9.3 ± 1.8 a	12.5 ± 1.9 a	5.5 ± 1.5 a
	Third	11.6 ± 1.8 b	13.9 ± 1.8 b	17.1 ± 2.0 b	5.5 ± 1.4 a
	Fourth	16.8 ± 1.6 a	19.8 ± 1.5 a	20.9 ± 1.2 a	4.1 ± 1.2 a
Five ($n = 7$)	First	0.9 ± 0.7 a	4.3 ± 1.1 a	9.3 ± 1.5 a	8.6 ± 1.3 a
	Second	5.7 ± 2.3 a	8.4 ± 2.1 a	11.3 ± 2.1 a	5.6 ± 1.4 a
	Third	8.9 ± 2.1 c	11.1 ± 1.9 c	13.9 ± 1.2 c	5.0 ± 1.3 a
	Fourth	12.6 ± 1.3 b	14.6 ± 1.5 b	17.7 ± 2.1 b	5.1 ± 1.3 a
	Fifth	16.3 ± 0.8	20.4 ± 1.3	20.9 ± 1.1	4.6 ± 1.1

Within a column data for the same wave in the three categories of number of waves per cycle with different letters (a–c) were significantly different ($P < 0.001$).

The length of the growing phase of the dominant follicle in the second wave (2.4 ± 0.9 days, $n = 31$) was lower ($P < 0.01$) than in first (3.3 ± 1.2 days, $n = 31$) and in the fifth (4.1 ± 1.2 days, $n = 7$) waves. In the third (2.7 ± 1.3, $n = 31$) and fourth (2.8 ± 1.3, $n = 26$) waves this length was similar ($P > 0.05$) to the others waves and independent of the number of waves per estrous cycle.

The average daily growth of the dominant follicles was 1.07 mm ($r^2 = 0.91$; $P < 0.001$; R.S.D. = 1.1; $n = 126$).

The mean length of the regression phase of the dominant follicle in the first wave (4.3 ± 1.4 days, $n = 31$) was longer ($P < 0.001$) than in the second (3.6 ± 1.1 days, $n = 31$), third (3.0 ± 1.3, $n = 26$) and fourth (3.1 ± 1.2, $n = 7$) waves.

In the regression phase of follicular waves (excludes the ovulatory wave), the dominant follicle had an average daily regression of 0.79 mm ($r^2 = 0.88$; $P < 0.001$; R.S.D. = 1.1; $n = 95$).

3.4. Preovulatory follicle and ovulatory wave: a comparison with the last wave of ovaries without ovulation

The onset of the last follicular wave in the estrous cycle was different ($P < 0.05$), and occurred earlier in the anovulatory ovary (15.1 ± 3.7 days, $n = 20$) than the ovulatory ovary (16.8 ± 1.4 days, $n = 20$) within a pair of ovaries. Similarly, the dominant follicle of the last wave of the anovulatory ovary reached its maximum diameter on day 16.7 ± 3.5 ($n = 20$) of the estrous cycle in contrast ($P < 0.001$) with that of the ovulatory ovary (day 20.0 ± 1.3, $n = 20$).

The length of the growing phase for the dominant follicle of the last wave was 1.7 ± 0.8 days in ovaries without ovulation ($n = 20$) and 3.1 ± 0.9 days in ovaries with ovulation ($n = 20$; $P < 0.001$).

The maximum diameter of the preovulatory follicle (7.1 ± 1.0 mm, $n = 20$) was greater ($P < 0.001$) than that of the dominant follicle of the last non-ovulatory wave (5.7 ± 0.4 mm, $n = 20$), and of all other dominant follicles (5.9 ± 0.8 mm, $n = 75$) identified.

The number of ovulations and the preovulatory follicle size were not related ($P > 0.05$). The number of preovulatory follicles was independent ($P > 0.05$) of the wave number of the estrous cycle.

4. Discussion

The interovulatory interval observed in Serrana goats (20.7 ± 1.0 days) was similar to that observed in other breeds (de Castro et al., 1999; González de Bulnes et al., 1999; Orita et al., 2000; Schwarz and Wierzchos, 2000; Padilla and Holtz, 2000; Medan et al., 2003).

The three to five follicular waves per estrous cycle, more frequently four waves, observed in this experiment was also similar to the results obtained by other researchers (de Castro et al., 1998, 1999; Medan et al., 2003). However, Schwarz and Wierzchos (2000) also reported six or seven waves per estrous cycle.

In the estrous cycles of Serrana goats with four follicular waves, the day of onset of each wave and maximum follicular diameter were similar to the data observed in Boer (Padilla and Holtz, 2000) and Saanen (de Castro et al., 1999) goats.

The day of onset of each follicular wave, the day of maximum follicular diameter and the end of the third and fourth follicular wave occurred earlier when the number of waves per estrous cycle increased. These differences began with the onset of the third wave (between day 8.9 ± 2.1 in goats with five waves and day 14.8 ± 1.3 in goats with three waves). The maximum plasma P4 concentration, observed by de Castro et al. (1999), was attained around day 10 and remained high at day 15. Additionally, a relationship between the high plasmatic P4 levels and the first and second follicular wave dynamics was recently observed in goats treated with exogenous P4 suggesting an acceleration in the follicular turnover (Menchaca and Rubianes, 2002). Although an effect of the CL number on the wave number per estrous cycle was not found in our study, further studies are necessary to evaluate the influence of daily plasma P4 concentration on the number of waves.

The duration of first interwave interval in Serrana goats (5.6 ± 0.3 days) was between the values observed in Boer goats (4.0 ± 1.4 days; Schwarz and Wierzchos, 2000) and in Saanen goats (7.3 ± 0.9 days; de Castro et al., 1999). In these studies, a longer first interwave interval relative to other interwave intervals was observed suggesting that this difference was probably due to lower, naturally occurring, plasma P4 concentration in the initial part of the estrous cycle. In our study, the interwave interval was longer when an ovulatory wave was observed. This observation supports the concept of indirect P4 action on follicular turnover and the fundamental role of natural luteolysis in ovulatory wave selection.

As in other studies (Ginther and Kot, 1994; de Castro et al., 1999), the maximum follicular diameter of the second wave was smaller than that of the first and fourth wave. However, in Serrana goats, the follicular diameter of the second wave was also smaller than that of the fifth wave. Additionally, the dominant follicle of the third wave was smaller than that observed in the fourth and five waves. These observation support the negative action of P4 on follicular growth suggested by Chemineau et al. (1988), and may be due to the differences in P4 plasmatic levels between the middle and the onset, or the end, of the estrous cycle as proposed by Ginther and Kot (1994). The shorter length of the growing phase of the dominant follicle in the second wave than the first and fifth waves and the greater length of the regression phase of the dominant follicle in first wave, with the exception of the fifth wave, also support these assumptions.

The onset of the last wave and the first day of maximum follicular diameter occurred later in the estrous cycle and with less variability in ovulatory ovaries than in anovulatory ovaries. The onset of the ovulatory wave (day 16.8 ± 1.4) coincided with the first day of the maximum follicular diameter of the last wave in anovulatory ovaries. This day was close to the day of luteolysis, and the occurrence of a recruitment and selection phase of preovulatory follicles following a prostaglandin application, which has been also observed by Maracek et al. (2002) in sheep. These results are also in accord with those obtained by Viñoles and Rubianes (1998) in Corriedale sheep. In this monovular breed, when estrous was induced by prostaglandin on Day 5 or 9 of the estrous cycle, the preovulatory follicle originated from the first follicular wave when the dominant follicle was in its growth phase or attaining maximum diameter. That study also observed that when the dominant follicle had entered its regression phase, the preovulatory follicle came from the second follicular wave.

Gonzalez-Bulnes et al. (2005) observed the prevalence of ovulatory follicles on the day of luteolysis induced with cloprostenol. However, in some cases of goats with double ovulations, the largest follicle was in the regressing phase and new ovulatory follicles were emerging.

Our results support the assumption that atresia occurs when the decrease in plasma P4 is simultaneous with the maximum diameter of dominant follicle. However, if the dominant follicle is in its growth phase, it will become ovulatory. The lower size of the dominant follicle of last follicular wave in the anovulatory ovaries reinforces the role of local effects in selection of the ovulatory wave, since the plasma P4 levels were the same for both ovaries.

In conclusion, the results of this study confirm that the pattern of follicular dynamics in goats is most frequently characterized by four waves. The phenomenon of follicular dominance was also present in the middle of the luteal phase. There was a great variability in the onset and duration of each wave during the estrous cycle. Similarly, the maximum size of the dominant follicle was very variable. The morphological and temporal differences hypothesised for the two last waves were verified with some similarity with the first wave, when the plasma P4 concentration was lower. Around Day 16 or 17 of the estrous cycle, several alterations in the characteristics of the follicular wave occurred. The onset of the ovulatory wave occurred after and with lower variability than the day of onset of the last wave of an anovulatory ovary suggesting a new wave was selected during natural luteolysis. These results support the deep involvement of progesterone in follicular dynamics. However, the regulating mechanisms of the last follicular wave of the estrous cycle remain to be clarified.

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