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Seasonal variation of the ovarian follicular dynamics and luteal functions of sheep in the subtropics

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Abstract

This study was undertaken to describe the development of individual follicles and corpora lutea (CL) in Ossimi ewe lambs at different seasons of the year in the subtropics. Seven ewe lambs underwent daily ultrasonographic examination for 20 interovulatory periods (IOP) during spring, winter and autumn. Ovarian follicles $\geq$2 mm and corpora lutea were counted and measured. Blood samples were taken for progesterone (P_4) analysis. All ewe lambs included, but one, were cyclic in all seasons studied. Three (65%) and two (35%) follicular waves were detected per estrous cycle. None of the characteristics of the large follicles was affected by season. Follicles $\geq$2 mm in diameter were significantly higher in winter. The CL developed slowly in autumn. Serum P_4 level was higher in autumn. Double ovulation was observed only in autumn. The data demonstrated that Ossimi sheep in the subtropics were cyclic in most seasons of the year. Season affected mainly the luteal functions with little influences on the follicular characteristics.

Keywords: Sheep; Subtropics; Follicle dynamics; Luteal function

1. Introduction

Understanding the pattern of ovarian follicular development is seen as an important step leading the development of techniques that maximize fertility in sheep. Also, studying seasonality in reproductive activity of subtropical breeds is important to determine the best breeding season for these breeds. It has been widely reported that the temperate breeds of sheep are seasonally polyestrous, while those originating from tropical areas showed estrous and breeding activity all the year around [1–6]. The situation is confused for the subtropical sheep, where seasonal variations in the length and intensity of light are not as great as they are in high latitude [7,8]. Reports on estrous and breeding activity of fat-tailed subtropical breeds of sheep vary greatly, with a general agreement of non-consistent estrous activity around the year [7,9–15]. Most of these data, however, have been mainly obtained either from the estrous activity or from the breeding ability of ewes at different times of the year. Whether these fluctuations of estrous activity and breeding efficiency are linked to similar variations in ovarian follicular dynamics and luteal functions is not yet clear.

The existence of dominance in sheep has attracted some debate. Basically, in cattle a functionally dominant follicle has the ability to inhibit the development of other competing follicles within both ovaries while continuing to thrive itself [16–18]. In sheep, follicles in a subsequent wave emerged after the largest follicle (LF) in the previous wave had stopped or about the same time as the end of the static of the largest follicle from the previous wave [4,19,20]. Also, follicle ablation increased FSH concentration and stimulated the growth of small follicles

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[21]. Other data would suggest that clear dominance does not occur in sheep [22–24].

Previous studies on sheep ovaries using gross and histological evaluation [25], laparotomy [26], endoscopy [4], or even the daily monitoring of follicles by ultrasonography [19–29] lead to controversial results. Whereas, some of these studies have shown convincingly that most estrous cycles in sheep have waves of follicular activities [4,19,21,28–30]. Others indicated that follicles in ewes grow and regress asynchronously or continuously [23,31–33].

The present study was undertaken to use daily ultrasound imaging of ovaries and hormonal analysis to describe and compare the patterns of ovarian antral follicle turnover and luteal functions of Ossimi ewe lambs throughout the estrous cycle at different seasons of the year in the subtropics.

2. Materials and methods

2.1. Animals and management

Seven clinically healthy Ossimi ewe lambs (a native subtropical fat-tailed breed), 13–15 months of age, and weighing 36–39 kg at the beginning of the experiment, were used. The animals were maintained indoor in the teaching hospital of the faculty of veterinary medicine, Assiut University (latitude 32°N and 27°E), under natural daylight and were provided with a diet adequate for maintenance. The experiment was carried out on the same group of animals over three different seasons: spring (May–June, $55.14 \pm 1\%$ relative humidity and 29.45 ± 0.3 °C maximum atmospheric temperature); autumn (September–October, $62.7 \pm 0.8\%$ relative humidity and 26.56 ± 0.3 °C maximum atmospheric temperature), and winter (January–February, $74.5 \pm 1.1\%$ relative humidity and 15.78 ± 0.3 °C maximum atmospheric temperature).

2.2. Ultrasonic examinations

In each season, daily transrectal ultrasonography was done for a complete interovulatory period (IOP) or for a maximum of 35 days, utilizing a real-time B-mode echo camera (Pie Medical, 100 LC, Maastricht, The Netherlands) connected to a 6/8 MHz changeable transducer. The transducer was fitted in a self-manufactured connector to favor its manipulation in the rectum. The transducer was manipulated externally, with the ewe in standing positing. At each examination, the number, diameter and relative position of all follicles $\geq$2 mm in diameter and corpora lutea (CL) were recorded and sketched on ovarian charts to analyze the pattern of growth or/and atresia. When a follicle or CL was not spherical a mean diameter was taken. Follicles were ranked into three size classes: small follicle (diameter 2 and 3 mm) medium-sized follicles (diameter 4 and 5 mm) and large follicles (diameter >5 mm).

2.3. Follicular data analysis

Days of ovulation (D0) were regarded as the days in which a large growing antral follicle that had been identified and followed for several days was no longer observed. Follicular wave was regarded as a group of follicles that grew from 2 or 3 mm to an ovulatory size of >5 mm in diameter. The largest follicle of a wave was defined as the one that grew to at least 5 mm and exceeded the diameter of all other follicles in the wave. If more than one follicle reached the same maximum size, the follicle that first attained the maximum diameter or remained at its maximum size for the longest period of time was regarded as the largest follicle of the wave. First ultrasonic detection of the LF as 2 or 3 mm in diameter was considered the day of emergence. The duration of growth of a follicle was the time taken by that follicle to grow from 2 or 3 mm in diameter to its maximum diameter. The growth rate (mm day^{-1}) was considered as the difference between maximum and minimum diameters of the ovulatory follicle divided by the duration of its growth. The duration of regression of a follicle was the time taken by that follicle to regress from its maximum diameter to 2 or 3 mm in diameter. The atretic rate (mm day^{-1}) was taken as the difference between maximum and minimum diameters of the LF divided by the duration of its atresia. The following characteristics of follicular waves for each ewe lambs were determined: (1) mean number of follicular waves; (2) mean maximum diameter attained by the LF of the wave; (3) mean growth and atretic rates of the LF of the wave; (4) mean number of small, medium-sized and large follicles.

2.4. Corpus luteum

The CL was examined daily and an image of the largest cross-sectional area was frozen and estimated. The first day of detection, growth rate, the day of maximum diameter, the first day of regression, and the regression rate were recorded. Incidence and diameter of the central cavity of the CL were also recorded whenever observed.

2.5. Intraovarian relationship

Data were grouped and tabulated to facilitate examination of: (1) frequency of development of the LF in the left and right ovaries; (2) frequency of follicular waves in which the LF and CL were in the same or opposite ovaries; and (3) relationship of location of a LF to location of the LF of the next wave.

2.6. Hormonal analysis

Blood samples were collected twice weekly parallel to D 0, 4, 7, 11, 14 and 0 of the IOP, by jugular venipuncture. Serum was harvested and stored at −20 °C until assayed. Circulating concentrations of progesterone (P_4) were determined by ELISA utilizing kits provided by Biosewoom Inc. (Sungdong-gu, Seoul, Korea, catalogue no. BS1405). The range of the standards used was 0.2–40.0 ng mL^{-1}. The inter- and intra-run precision had a coefficient of variation of 2.9 and 4.8%, respectively.

2.7. Statistical analysis

Data were normalized to days of ovulation for analysis and presentation. Analysis of variance (ANOVA) was used for comparison among seasons for follicular, luteal and hormonal data, while *t*-test was used for comparison between ewes with two or three waves per cycles. Follicular, luteal and hormonal data were also analyzed for period effects using repeated measure analysis of variance, with Fisher's protected least significant difference (LSD) as the post-ANOVA test [34]. Goodness-of-fit chi-square analyses were used to detect frequencies that differed from equality. Frequency distributions were examined by chi-square for differences among wave categories. Similar analyses were used to determine whether the largest follicle and the corpus luteum occurred more frequently on the same or the opposite ovary. Relationships between location of a largest follicle and location of the next one were examined by chi-square goodness-of-fit and frequency distribution analyses. Data were expressed in mean ± S.E.M. and the significance was set at $P < 0.05$.

3. Results

All the ewe lambs were cycling in all studied seasons yet one (in winter) was excluded from the analyses as she had a persistent CL. Complete ovarian follicular data were obtained for 20 interovulatory periods during spring ($n = 7$), autumn ($n = 7$), and winter ($n = 6$). Based on the definition used for the follicular wave, three (13/20, 65%) and two (7/20, 35%) follicular waves were detected per IOP (Fig. 1). None of the characteristics of the largest follicle of the first (LF1), second (LF2) or third (LF3) follicular waves were affected by the season (Table 1). Number of waves per cycle affected certain patterns of follicular characteristics (Table 2).

The number of small, medium and large follicles were aligned with the beginning and end of an average length of 17 days for the cycle with three waves and 14 days for cycle with two waves (Fig. 2). The mean daily number of all follicles ≥2 mm in diameter was significantly ($P = 0.008$) higher in winter (5.29 ± 0.2) than in spring (4.27 ± 0.2) or autumn (4.57 ± 0.2). In cycles with three waves, a significant ($P = 0.01$) day effect was observed for the mean daily number of small follicles. A numerical, but not significant, increase was seen for the mean number of the medium-sized follicles. The mean daily number of large follicles varied significantly among days of the IOP ($P = 0.0001$). Similar fluctuations of the mean follicular number were seen in cycles with two waves (Fig. 2). However, these fluctuations did not approach the significance level for the small and medium follicles, but was significant for the large ones ($P = 0.01$).

The effect of season on luteal function is shown in Table 3. The CL developed slowly ($P = 0.04$) achieved maximum diameter later ($P = 0.02$) and started to regress later ($P = 0.05$) in autumn. Regression rate of the CL was significantly slower in winter ($P = 0.006$). It appeared ($P = 0.03$) and regressed ($P = 0.01$) significantly earlier in animals with two waves per cycle than in those with three waves. Double ovulation was

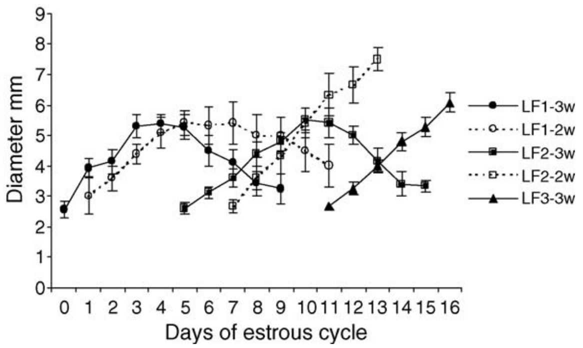

Fig. 1. Turnover of the large follicles in cycles with three or two follicular waves. LF1-3w, LF2-3w, LF3-3w: the large follicles of the first, second and third waves in cycles with three waves, respectively. LF1-2w, LF2-2w: the large follicles of the first and second waves in cycles with two waves. 0: day of ovulation. Values in means ± S.E.M.

Table 1
Effect of season on follicular characteristics throughout an entire IOP in Ossimi ewe lambs

Characteristics	Season			Total ($n = 20$)
	Spring ($n = 7$)	Autumn ($n = 7$)	Winter ($n = 6$)	
IOP	17.0 ± 0.7^{a}	17.0 ± 0.9^{a}	15.5 ± 1.0^{a}	16.55 ± 0.5
Waves/IOP				
(2)	2	2	3	7
(3)	5	5	3	13
LF1				
Emergence (day)	-0.3 ± 0.4^{a}	0.0 ± 0.5^{a}	0.0 ± 0.3^{a}	-0.1 ± 0.2
GR (mm day^{-1})	1.21 ± 0.2^{a}	1.05 ± 0.2^{a}	1.28 ± 0.2^{a}	1.18 ± 0.1
MD (mm)	6.21 ± 0.4^{a}	5.9 ± 0.3^{a}	6.33 ± 0.2^{a}	6.14 ± 0.2
DMD	3.71 ± 0.2^{a}	4.43 ± 0.7^{a}	3.67 ± 0.6^{a}	3.89 ± 0.3
DA	5.57 ± 0.6^{a}	6.57 ± 0.7^{a}	5.67 ± 0.7^{a}	5.95 ± 0.4
AR (mm day^{-1})	0.92 ± 0.1^{a}	1.08 ± 0.1^{a}	0.77 ± 0.1^{a}	0.93 ± 0.1
LF2				
Emergence (day)	5.86 ± 0.6^{a}	5.57 ± 0.4^{a}	6.67 ± 0.7^{a}	6.0 ± 0.4
GR (mm day^{-1})	0.79 ± 0.1^{a}	0.84 ± 0.1^{a}	1.07 ± 0.1^{a}	0.89 ± 0.1
MD (mm)	6.07 ± 0.3^{a}	6.21 ± 0.5^{a}	7.18 ± 0.4^{a}	6.46 ± 0.3
DMD	10.71 ± 0.8^{a}	10.57 ± 0.9^{a}	11.3 ± 0.6^{a}	10.85 ± 0.5
DA	11.0 ± 0.8^{a}	11.8 ± 0.9^{a}	12.3 ± 0.2^{a}	11.62 ± 0.4
AR (mm day^{-1})	0.93 ± 0.01^{a}	0.6 ± 0.04^{a}	1.3 ± 0.2^{a}	1.08 ± 0.08
LF3				
Emergence (day)	11.4 ± 0.2^{a}	11.6 ± 0.5^{a}	12.3 ± 0.6^{a}	11.7 ± 0.3
GR (mm day^{-1})	0.88 ± 0.1^{a}	0.89 ± 0.04^{a}	0.93 ± 0.1^{a}	0.9 ± 0.1
MD (mm)	6.3 ± 0.3^{a}	5.08 ± 1.0^{a}	5.83 ± 0.1^{a}	5.7 ± 0.4
DMD	16.8 ± 0.2^{a}	16.2 ± 0.8^{a}	15.7 ± 0.8^{a}	16.3 ± 0.3

IOP: interovulatory period; LF1, LF2 and LF3: largest follicle of the first, second and third follicular waves; GR: growth rate; MD: maximum diameter; DMD: day of maximum diameter; DA: day of atresia; values with different superscript letter in the same row differ significantly. Data in mean ± S.E.M.

observed in three ewe lambs (15%), all in autumn. Corpora lutea with central cavities were detected in 7 of the 21 CL (33.3%). These cavities were firstly observed on D 3.4 ± 1.5 (range D 1–4), their diameters ranged between 5.0 and 7.5 mm at first detection (average 5.9 ± 0.6 mm), which gradually decreased as the cycle advanced, to disappear completely on mean D 9.0 ± 1.5 (range D 5–12).

The data of the serum P_4 concentrations were normalized for the day of ovulation (D 0). The level was higher in autumn than in the other two seasons studied (Table 3), but the significant level reached only on D 11 ($P = 0.04$). The P_4 concentration was significantly higher in 3-wave cycles than in 2-wave cycles on D 14 (3.5 ± 1.5 versus 1.5 0.3 ng mL^{-1}, $P = 0.03$). There was no significant difference in the serum P_4 concentrations between animals with compact or cystic CL.

A total of 32 single ovulations were observed during the 20 IOP of the 7 lambs. Ovulations were distributed equally (16:16) between the right and left ovaries. The number of the largest follicles located in the left ($n = 25$) versus the right ovary ($n = 29$) did not differ significantly among wave categories. The frequency in which the largest follicles were in the same (15/46, 32.6%) versus the opposite (31/46, 67.4%) ovary to the CL did not differ significantly ($P = 0.09$). The largest follicles were located in the same ($n = 18$) or opposite ovary ($n = 13$) to the previously largest follicle in almost equal frequencies.

4. Discussion

This study seems to be the first one which characterized daily and seasonally the ovarian follicular dynamics and luteal functions of Ossimi breed of sheep in the subtropics. Based on the current approach (ultrasonic examinations and hormonal analysis), it could be confirmed that this breed of sheep was almost cyclic in all seasons studied, supporting other studies on mid-Egypt Ossimi flock [8,35]. Seasonal variations of the cycle length lacked any significance, supporting the report on native Barki ewes [15]. The total number of follicles ≥2 mm in diameter observed here differed

Table 2
Effect of number of waves per IOP on follicular characteristics of Ossimi ewe lambs

Characteristics	Number of waves/IOP	
	Two waves ($n = 7$)	Three waves ($n = 13$)
IOP	14.3 ± 0.6^a	17.77 ± 0.4^b
LF1		
Emergence (day)	0.29 ± 0.3^a	-0.31 ± 0.3^a
GR (mm day^{-1})	1.26 ± 0.2^a	1.14 ± 0.1^a
MD (mm)	6.36 ± 0.2^a	6.02 ± 0.3^a
DMD	4.71 ± 0.8^a	3.54 ± 0.3^a
DA	6.71 ± 0.8^a	5.54 ± 0.5^a
AR (mm day^{-1})	0.79 ± 0.1^a	1.0 ± 0.1^a
LF2		
Emergence (day)	7.29 ± 0.7^a	5.31 ± 0.3^b
GR (mm day^{-1})	1.05 ± 0.2^a	0.8 ± 0.1
MD (mm)	7.36 ± 0.4^a	5.97 ± 0.2^b
DMD	12.71 ± 0.8	9.85 ± 0.3^b
DA	–	11.62 ± 0.4
AR (mm day^{-1})	–	1.08 ± 0.1
LF3		
Emergence (day)	–	11.69 ± 0.3
GR (mm day^{-1})	–	0.9 ± 0.01
MD (mm)	–	5.72 ± 0.5
DMD	–	16.31 ± 0.4

IOP: interovulatory period; LF1, LF2 and LF3: largest follicle of the first, second and third follicular waves; GR: growth rate; MD: maximum diameter; DMD: day of maximum diameter; DA: day of atresia; values with different superscript letter in the same row differ significantly. Data in mean ± S.E.M.

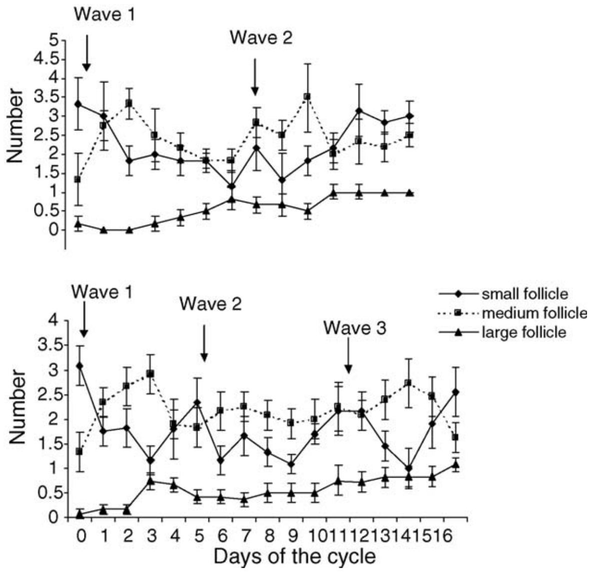

Fig. 2. Changes in follicular population throughout an entire interovulatory period in ewe lambs with two ($n = 7$, upper panels) and three waves ($n = 13$, lower panels) per IOP. Values in mean ± S.E.M.

significantly among seasons, the number was significantly higher in winter. Contrasting result was reported in other breed of sheep, where the mean number of follicles did not vary significantly among seasons [4]. Others found more small follicles during anestrous than during the breeding season [36].

Season affected the CL morphologically (size) and tend to affect it functionally (peripheral P_4 level).

Table 3
Effect of season on luteal function throughout an entire IOP in Ossimi ewe lambs

Characteristics	Season			Total ($n = 20$)
	Spring ($n = 7$)	Autumn ($n = 7$)	Winter ($n = 6$)	
CL				
Detection (day)	2.57 ± 0.2^a	1.86 ± 0.4^a	1.67 ± 0.6^a	2.05 ± 0.3
GR (mm day^{-1})	1.43 ± 0.2^a	0.69 ± 0.2^b	1.04 ± 0.4^{ab}	1.05 ± 0.2
MD (mm)	12.7 ± 0.4^a	13.82 ± 0.6^a	13.7 ± 0.5^a	13.39 ± 0.3
DMD	5.43 ± 0.6^a	8.57 ± 0.5^b	6.0 ± 1.0^a	6.7 ± 0.5
DR	11.57 ± 1.2^a	14.57 ± 0.9^b	12.2 ± 0.5^a	12.8 ± 0.6
RR (mm day^{-1})	1.78 ± 0.3^a	1.91 ± 0.3^a	0.92 ± 0.1^b	1.57 ± 0.2
Double CL (n)	$0/7^a$	3/7	$0/6^a$	3/20
Cystic CL (n)	$1/7^a$	$4/10^a$	$2/6^a$	7/23
P_4 (ng mL^{-1})				
D 0	0.7 ± 0.1^a	0.83 ± 0.1^a	0.6 ± 0.1^a	0.73 ± 0.1
D 4	2.96 ± 0.5^a	3.03 ± 0.6^a	1.8 ± 0.6^a	2.62 ± 0.4
D 7	4.0 ± 0.4^a	5.92 ± 1.4^a	3.74 ± 0.3^a	4.64 ± 0.6
D 11	3.72 ± 1.0^a	6.0 ± 0.8^b	3.4 ± 0.8^a	4.37 ± 0.6
D 14	1.03 ± 0.2^a	3.87 ± 0.9^b	2.7 ± 0.7^b	2.68 ± 0.5
D 0	0.5 ± 0.1^a	0.8 ± 0.2^a	0.7 ± 0.1^a	0.73 ± 0.1

CL: corpus luteum; GR: growth rate; MD: maximum diameter; DMD: day of maximum diameter; DR: day of regression; D 0: day of ovulation. Values with different superscript letter in the same row differ significantly ($P < 0.05$). Data in mean ± S.E.M.

Autumn seemed to be the most favorable season for the function of the CL. In previous studies, the progesterone concentrations were higher in the second cycle of the season and it increased over subsequent luteal phases [22]. The Ossimi breed characterized by low fecundity [35], which is supported by the low ovulation rate reported here. One-third of the CL were detected with central cavities, which is slightly lower than that observed (42%) in a similar study in sheep [37]. On the basis of this and the previous study, it seemed that both conditions of the CL (compact or with a central cavity) are similar in function, as the peripheral levels of P_4 were approximately similar. The growth and regression pattern of the CL as well as the serum P_4 concentrations differed among lambs with two or three waves per cycle. The life span of the CL was shorter, the size was smaller and the P_4 levels during the second-half of the cycle were lower in ewe lambs with two waves.

Several observations in the present study would support the theory of dominance in sheep: first, within each wave one follicle grew larger than the others. Second, the emergence of successive waves only occur after the demise of the largest follicle in the previous wave. Third, the small-sized follicles showed beaks of growth at times constant with the follicular emergence. Two and three follicular waves were recorded in each cycle, which is constant with some previous studies [4,29]. Two to four waves per cycle were observed by others [19,20,24].

The tendency for ovulation to take place more often in the right or left ovary is not proven. Also, no relationship was found between the locations of the largest follicles of the different waves or between the location of the CL and the largest follicles. Controversial observations were reported in heifers and sheep [25,38–41].

In conclusion, the present data obtained in subtropical ewe lambs confirm that this breed of sheep is almost cyclic in all seasons studied. Season affected mainly the luteal functions with little influences on the follicular characteristics. The data also strongly support the conclusion that the development of ovarian follicles in sheep occurs in a wave-like pattern, with a predominance of three waves per cycle. Number of waves per cycle affected certain patterns of follicular and luteal developments.

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