Relationship between follicle growth and circulating gonadotrophin levels during postnatal development of sheep

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Abstract

This study investigates the number and size of ovarian antral follicles in relation to plasma follicle stimulating hormones (FSH) and luteinizing hormone (LH) concentrations from birth to 26 weeks of age in ewe lambs of the Ouled Djellel breed, a non-seasonal breed of sheep. Plasma was collected from 10 ewe lambs at 14 sampling times (Week 0, i.e. <24 h, Week 1 and every two weeks from Week 4 to Week 26, inclusive). At each of these stages, four ewe lambs were slaughtered, the ovaries recovered and weighed, and the number and size of the follicles determined from histological examination. The pattern for plasma FSH showed a peak at Week 10, a smaller peak at Week 18 and a very small peak at Week 24. The pattern for LH was similar until Week 24 when the largest peak occurred. Paired ovarian weight increased rapidly from birth to four weeks and then more slowly to 10 weeks, followed by a decline at 12 weeks and a gradual increase from 14 to 24 weeks of age. The number and total diameter of follicles ≥3 mm in diameter showed similar patterns of development – rising gradually from birth to Week 14, falling to Week 16 and then rising more rapidly to a peak at Week 24. Maximum follicle diameter declined from birth to Week 1, then rose rapidly to Week 4, followed by a more gradual rise to Week 14 and, thereafter, a more rapid increase to a peak of 7.23 ± 0.16 mm at 24 weeks old. The number of follicles (<3 mm diameter) increased rapidly from birth to Week 10 and then declined to values similar to those at Weeks 1 and 4. First behavioural oestrus was observed at Week 24 and a corpus luteum was present on the ovary of one lamb at Week 24 and two lambs at Week 26. It was concluded that two or three peaks in plasma FSH and LH levels precede puberty and first

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ovulation in Ouled Djellel ewe lambs, and first ovulation occurred at 24–26 weeks of age. The increase in follicle number and size generally reflected the pattern of plasma FSH and LH levels.

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1. Introduction

Follicle stimulating (FSH) and luteinizing (LH) hormones are required for follicular growth, maturation and steriodogenesis in ovarian mammals. The subject has been reviewed for different species (Fortune, 1994; Driancourt, 1991; Elizabeth et al., 2000; Driancourt, 2001; Evans, 2003). Postnatal development of ovaries and the variations in FSH and LH during this period of life are of great importance in determining reproductive capacity in all mammals.

Postnatal ovarian follicular development has been previously studied in ewe lambs of different genotypes and ages. Large numbers of vesicular follicles have been observed in the ovaries of new-born lambs (Mansour, 1959; Land and McGovern, 1968; Land, 1970). Based on post-mortem observations every four weeks, from 4 to 24 weeks, and at 33 weeks of age in Merino ewe lambs, the numbers of vesicular follicles declined between 4 and 12 weeks after birth and then did not change from 12 to 33 weeks of age (Kennedy et al., 1974). In a study of ewe lambs from birth to 10 weeks of age, a peak number of antral follicles were seen at four weeks of age while growing follicles were most numerous at two weeks of age (Tassel et al., 1978). In a more recent study using transrectal ovarian ultrasonography every two weeks from 4 to 24 weeks of age in prepubertal Suffolk × Western Face ewe lambs, only the numbers of antral follicle ≥3 mm were examined. Numbers increased from 14 to16 weeks, decreased between 16 and 18 weeks and then rose again between 22 and 24 weeks after birth (Bartlewski et al., 2002).

None of these studies was investigated the size variation in follicles at different ages from birth to first ovulation. In addition, there is little information on changes in ovarian weight and growth pattern of antral follicle of different diameters, ≥1 and <2 mm, ≥2 and <3 mm, and ≥3 mm, in relation to changes in FSH and LH peripheral concentrations during postnatal development in sheep. The aim of this study was to examine the pattern of variation in antral follicular growth at different diameters during postnatal period in non-seasonally Ouled Djellel ewe lambs and its relationship with circulating levels of FSH and LH.

2. Materials and methods

2.1. Experimental animals

Studies were carried out on 140 ewe lambs born in late September 2003 from three to four-year-old Ouled Djellel sheep reared at the experimental station in Ain Mlila (36° 03′ N, 6° 57′ E), Oum El Bouaghi, Algeria. Estrus cycle of the mothers had been synchronized by a 14-day treatment with intra-vaginal sponges containing 40 mg flurogestone acetate. This synchronization afforded the opportunity to obtain blood samples from a definite number of ewe
lambs that had approximately the same date of birth. After weaning at 16 weeks of age, the ewe lambs remained under natural conditions throughout the study. The ewe lambs were fed according to a standard ration. Four ewe lambs were slaughtered and blood collected at 0 (<24 h), 1, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24 and 26 weeks. The ovaries were weighed, fixed in Bouin–Holland’s solution, embedded in paraffin wax and serially sectioned at a thickness of 10 μm. All sections were mounted and the slides were stained with haematoxylin and eosin, and examined using light and a projection microscope. In both ovaries, the number of antral follicles ≥1 and <2 mm, ≥2 and <3 mm, and ≥3 mm in diameter, total and maximum follicle diameters of all follicles ≥3 mm in size were counted. The nucleus of the ovum was used as a marker. The diameter of all antral follicles was measured microscopically using the mean of two measurements. In addition, the diameter of the largest follicle was measured macroscopically (Tassel et al., 1978). In the absence of follicles ≥3 mm in diameter, the maximal follicular diameter was calculated. The boundary of the follicle was defined by the layer of the membrana granulosa.

Plasma concentrations of FSH and LH were determined in blood samples taken from 10 ewe lambs at 0 (<24 h), 1, 4, 6, 8, 10, 12, 14, 16, 18, 20, 22, 24 and 26 weeks. The 10 ewe lambs sampled on each occasion were selected at random and included the four animals that were slaughtered at that age. Each lamb was sampled only once. Blood samples were collected into 10 ml heparinized vacutainers from the jugular vein, always between 9:00 and 10:00 am and only once for each sampling period. After centrifugation (800 g, 15 min), plasma was stored at −20 °C until analysis. Only animals that showed normal growth in weight were included in this study.

2.2. Hormone assays

Plasma concentrations of FSH and LH were determined at the hormonal assay laboratory of the Research Unit UMR6175 (Physiology of Reproduction and Behavior, INRA, Nouilly, France).

FSH was determined by a radioimmunoassay (RIA) kit supplied by the National Hormone and Pituitary Programme (NHPP) of the National Institute of Diabetes and Digestive and Kidney Diseases (NIDDK). The ovine FSH (oFSH) used for iodination was oFSH NIDDK-oFSH-I-SAIFP-2 AFP-4117A. The oFSH reference preparation was NIH-oFSH-RP2-4117A, a gift of Dr. Parlow and the oFSH antiserum was anti oFSH NIDDK-anti-oFSH (AFP-C5288113). The final FSH antiserum dilution was 1/80,000. Plasma volume was 100 μl and each sample was assayed in duplicate. The standards and standard curve samples were prepared in hypophysectomized ewe plasma. The sensitivity of the assay was 0.1 ng/ml. The range of the standard curve was 0.1–6.4 ng/ml. The intra- and inter-assay coefficients of variation (CVs) were between 10.6 and 9.5%, with mean concentration between 1.5 and 1.53 ng/ml, respectively.

LH was measured by sandwich enzyme-linked immunosorbent assay (Elisa) (Spearow and Trost, 1987) developed and validated in UMR6175. Immuno Nunc Maxisorp plates C96 (446612) were coated with 100 μl per well of the first monoclonal anti-β oLH518B7 antibody (Matteri et al., 1987) working dilution [1/3200 in carbonate; 50 mM, pH 9.6]. Plates were stored overnight at 4 °C. This antibody was obtained from Dr. Jan Roser, Department of Animal Science, University of California, Davis, CA, USA. Antibody-coated plates were rinsed three times with 450 μl per well of wash buffer (PBS 10 mM, NaCl 150 mM, Tween 0.1%, pH 7.4) using a LP41 Adill washer. Then, 150 μl of saturated buffer [wash buffer/Sea-Block (Pierce, 37527 or Uptima), 7:1, v/v] was added per well for 1 h at 37 °C. Thereafter, the plates were rewashed with wash
buffer. Next, 80 μl of diluted buffer [wash buffer/Sea-Block/2% normal serum rat, 7:1:2, v/v] was added per well plus 20 μl of plasma sample or standard and controls, singly or in duplicate, using an automate multiprobe. Standard ovine LH (oLH) was provided by Dr. Yves Comparnous (UMR6175), Nouilly, France. This standard (lot 1083) was diluted in zero ewe plasma. The range of the standard curve was 0 point and from 0.1 to 6.4 ng/ml. Plates were washed after incubation at 4 °C overnight. Thereafter, 100 μl of the second biotinylated monoclonal anti-α antibody (Serotec MCA 1026) (Dirnhofer et al., 1994), a solution (500 μg/ml) diluted to 1/2200 in wash buffer and normal rat serum (1%, v/v) was added per well and incubated for 1 h at 37 °C. After washing, 100 μl of neutravidin-conjugated to horseradish peroxidase (HRP; Pierce, 31001), 1 mg/ml was diluted to 1/4000 in wash buffer. Plates were incubated at 25 °C in darkness. The plates were again washed and 100 μl of TMB KPL (tetramethylbenzidine) (Sureblue, ref. 52-00-02) was added to all wells. The color reaction was allowed to develop for 25 min in the dark. The enzyme reaction was stopped by adding 50 μl per well of acid solution (distilled water/HCl/sulphuric acid, 6:1:1, v/v). Afterwards, the optical density of each well was read at 450–620 nm on a Spectracount. The intra- and inter-assay coefficients of variation (CVs) were between 11.3 and 7.9%, respectively, with mean LH concentrations of 0.8 ng/ml.

2.3. Data analysis

The follicular and weight data were analyzed on a per ewe basis (data from both ovaries of each ewe were combined) and the following mean values were calculated: (1) paired ovarian weight; (2) total number of antral follicles ≥1 and <2 mm, ≥2 and <3 mm, and ≥3 mm in diameter; (3) total follicle diameter; (4) maximum follicle diameter of all follicles ≥3 mm. The means for ewes and peripheral plasma concentrations of FSH and LH (mean ± S.E.M.) from birth to 26 weeks of age were analyzed by Anova (Statistica Version 5.1, StatSoft France, 1997). Multiple comparisons were made using the method of Neuman–Keuls for post-Anova multiple comparisons (P < 0.05). All data are presented as means ± S.E.M.

3. Results

3.1. Circulating FSH and LH

Pattern of plasma FSH showed a peak at 10 weeks of age, a second lower peak at 18 weeks and a very small peak at 24 weeks of age (Fig. 1). At birth, the FSH level was low (0.3 ± 0.05 ng/ml) and the level rose slowly to six weeks of age followed by a more rapid rise to the first peak at 10 weeks (3.0 ± 0.51 ng/ml; P < 0.0001). The level of FSH fell between 10 and 12 weeks, then rose slightly until 16 weeks, followed by a faster rise to 18 weeks (2.4 ± 0.25 ng/ml; P < 0.05). Thereafter, the value fell to a level similar to that at 12 weeks old, but there was the suggestion of a further peak at 24 weeks of age. The pattern of plasma LH was very similar to that for FSH with peaks at 10 and 18 weeks of age, but the peak at 24 weeks was very prominent (Fig. 1). LH was initially detected at Week 1 and the level remained close to zero until six weeks, after which it rose to a peak value of 1.7 ± 0.37 ng/ml at 10 weeks, followed by a fall to 0.4 ± 0.15 ng/ml at 16 weeks, then a slight rise to a peak at 18 weeks and a further fall until 22 weeks old. The level then rose to 3.4 ± 0.48 ng/ml at 24 weeks (P < 0.00002), a mean LH increase of 6.6-fold from the preceding sampling age. This significant increase represents the preovulatory LH surge, which is supported by the presence of a corpus luteum on the ovary of one lamb at 24 weeks and two lambs at 26 weeks of age; the first behavioural oestrus was observed at 24 weeks old.
3.2. Paired ovarian weights

The weight of paired ovaries rose very quickly between Weeks 1 and 4 ($P < 0.0002$) and there was a further rise between Weeks 4 and 10 (Fig. 2). The weight then fell at 12 and 14 weeks.
Fig. 3. Mean (±S.E.M.) follicle numbers of all follicles ≥3 mm in diameter in both ovaries of four Ouled Djellal ewe lambs slaughtered at 0 (<24 h), one week and every two weeks from 4 to 26 weeks of age. Values with different letters are significantly different (P < 0.05).

(P < 0.03) to a value similar to that attained at four weeks old. Paired ovarian weight rose between 14 and 16 weeks and remained at a similar level until 20 weeks, when it rose again to a further plateau at 22–26 weeks.

3.3. Number of antral follicles at different sizes, total diameter of follicles ≥3 mm in diameter, and maximum diameter of follicles

The pattern in relation to age of lamb was very similar for the number (Fig. 3) and total diameter (Fig. 4) of follicles ≥3 mm in diameter. There was a steady rise in these values from birth to 14 weeks old (0.0 ± 0.00–2.5 ± 0.29 follicles and 0.0 ± 0.00–9.0 ± 1.08 mm, P < 0.05), a significant fall between 14 and 16 weeks (P < 0.003), followed by a rapid rise between 16 and 18 weeks old (1.0 ± 0.00–4.5 ± 0.29 follicles and 3.2 ± 0.05–17.4 ± 0.86 mm, respectively). After a small fall to Week 20, there was a further rise to a peak at 24 weeks (5.5 ± 0.64 follicles and 23.1 ± 1.97 mm, respectively), followed by a significant fall (P < 0.0008) by 26 weeks of age. The maximum mean follicle diameter decreased from birth to Week 1 (P < 0.05); thereafter, the pattern for this variable was broadly similar to the number and total diameter of follicles ≥3 mm (Fig. 5). There was an indication of a peak around Week 12, again at Week 20 and the highest value was observed at Week 24. The maximum diameter reached 4.9 ± 0.25 mm at Week 18 and 7.2 ± 0.16 mm at 24 weeks old. These two increases in maximum antral follicular diameter corresponded to the increase in plasma concentrations of both FSH and LH at 18 weeks of age, and to the peak of LH at 24 weeks of age.
levels seen at birth and four weeks of age. Number of follicle $\geq 1$ and $<2$ mm at 18 weeks was similar (15.2 $\pm$ 1.10 follicles, $P > 0.05$) to that recorded at 4 and 26 weeks of age. Note that the high concentration of FSH and LH at 10 weeks of age corresponded to the significant increase in number of follicle $\geq 1$ and $<3$ mm in diameter.

Fig. 4. Mean ($\pm$S.E.M.) total follicle diameter of all follicles $\geq 3$ mm in diameter in both ovaries of four Ouled Djellel ewe lambs slaughtered at 0 (<24 h), one week and every two weeks from 4 to 26 weeks of age. Values with different letters are significantly different ($P < 0.05$).

Fig. 5. Mean ($\pm$S.E.M.) maximum diameters of antral follicles reached in both ovaries of four Ouled Djellel ewe lambs slaughtered at 0 (<24 h), one week and every two weeks from 4 to 26 weeks of age. Values with different letters are significantly different ($P < 0.05$).
4. Discussion

There are no published reports on variations in gonadotropin levels in relation to follicle development from birth to age of puberty in sheep. The results of the present study show that the growth pattern of antral follicles was correlated with variations in circulating FSH and LH levels...
from birth to first ovulation in Oulled Djellel sheep and that there were two or three peaks of FSH and LH before first ovulation.

The early rise in both FSH and LH from birth to 10 weeks of age is more closely correlated to an increase in ovarian weight and numbers of antral follicles <3 mm in diameter than to the increase in follicles >3 mm in diameter. This rise in follicle development was due to the increase in FSH after birth, which, reaching a certain threshold level, stimulated growth of antral follicles (Fry and Driancourt, 1996) and influenced the rate of growth and health of preantral follicles in ewe lambs (Campbell et al., 2004). Basal follicular growth in sheep can occur in the absence of gonadotrophins (Dufour et al., 1979; Driancourt et al., 1987) but growth is mainly under the control of growth factors of paracrine origin (Monniaux, 1997), where FSH may exert an indirect mitogenic effect on granulosa cells by enhancing expression of growth factors or growth factor receptors. Moreover, follicles measuring 0.8–2 mm in diameter are gonadotrope-sensitive and are mobilized when exogenous gonadotropins are injected (Driancourt et al., 1993). In addition, FSH receptors were detected in ewe lambs in the earliest stage of follicular growth (Tisdall et al., 1995). In Shropshire ewe lambs, the first peak in LH and FSH at 10 weeks was due to the onset of pulsatile secretion of LH about 11 weeks after birth (Foster et al., 1975a,b) and pulsatile secretion of FSH at 5–10 weeks of age (Rawlings and Churchill, 1990). Interestingly, the increase in numbers of follicles ≥2 mm from birth to 10 weeks of age correlated with the increase in both FSH and LH and led to increased ovarian weight. Therefore, the increase in ovarian weight is due, in part, to the increase in the number and size of antral follicles. This finding is in agreement with the report that ovarian weight increased between two and eight weeks of age with an increase in the number and size of vesicular follicles (Tassel et al., 1978) in ewe lambs. However, the growth of follicles beyond 2 mm in size (tonic growth of follicles) was acutely gonadotrophin-dependent in sheep (Driancourt, 1991; Driancourt et al., 1985, 1993; Fortune, 1994), and these gonadotropin-dependent follicles regress when ewe lambs were hypophysectomized (Driancourt et al., 1993). In addition, at this follicular size, the number of FSH receptors on the granulosa cells and LH receptors on the theca layer are at a maximum (Carson et al., 1979) and aromatase activity is detectable in granulosa cells (Tsonis et al., 1984).

After 10 weeks of age, there was an increase in the number of follicles ≥3 mm, total and maximum follicle diameters and a decrease in the number of follicles <3 mm in diameter. It is well known that in sheep the size at follicle recruitment is 2 mm in diameter (Driancourt, 2001; McNeilly et al., 1982; Picton et al., 1990; Campbell et al., 1998) and FSH is the key hormone inducing recruitment (Picton et al., 1990). There is also a minimal threshold of FSH concentration below which recruitment cannot proceed and there are also variations in the FSH threshold between follicles in a specific ewe (Fry and Driancourt, 1996).

The second peak of both FSH and LH at 18 weeks is correlated with the increase in number of follicles ≥3 mm and maximum follicle diameter at this age, as ewe lambs approach first ovulation. This observed increase can be explained by the increase in LH pulse frequency (Rawlings and Churchill, 1990) and by the growth of follicles to a size greater than 4 mm in diameter. Follicles with this size had expressed and developed LH receptors (Driancourt, 2001). Previous studies have demonstrated that FSH induced LH receptors in granulosa cells (Zeleznik et al., 1974; Carson et al., 1979) and that functional theca and granulosa LH receptors and an active aromatase system were present (McNatty et al., 1987). It appears that the increase in number, size and maximum follicle diameter from 18 weeks to first ovulation may be driven by increased bioavailability of FSH, which induced onset of puberty in ewe lambs (Padmanabhan et al., 1992) and can explain the small increase of FSH at 24 weeks of age. Indeed, both gonadotropin hormones stimulate ovarian
follicular growth as shown by the size increase in maximum follicle diameter to ovulatory-sized follicles at puberty.

The third peak of LH and small increase in FSH was correlated with the increase in number, total size, and maximum follicle diameter at 24 weeks after birth. The increase in these parameters might be stimulated by an increase in the frequency of LH pulses prior to first ovulation (Ebling et al., 1990; Rawlings and Churchill, 1990). These results are in agreement with a previous report that an increase in serum gonadotropin levels occurred at puberty and this reflected the critical events culminating in first ovulation in sheep (Kathleen et al., 1991). Therefore, this increase forced the LH surge, which resulted in ovulation, as shown by the presence of corpus lutea. The continuity of growth of antral follicles was maintained by both FSH and LH, and that, in sheep, the growth and development of ovarian follicles from late preantral (Campbell et al., 2004) to the preovulatory stage (Webb et al., 1999) was regulated by both LH and FSH. Moreover, follicles >4 mm in diameter contain high and low levels of oestradiol and testosterone, respectively (Carson et al., 1981), while P450 aromatase was detected only in granulosa cells from ovine follicles >3.5 mm in diameter (Huet et al., 1997). This enzyme is a key maturational step as it enables the follicle to produce oestradiol from androgen precursors produced by theca cells. Therefore, as animals approached first ovulation and follicles increased in number and total diameter, more oestradiol was secreted to induce a preovulatory LH surge and ovulation (Foster et al., 1984; Keisler et al., 1985). By this time, the gonadotropin surge had also attained a sensitivity comparable to or greater than that of an adult to the stimulatory feedback action of estradiol (Foster, 1984) and permitted the first ovulation to occur around 24–26 weeks of age, as shown by the presence of corpus lutea. The LH ovulatory peak was not recorded, as this peak lasts 8–10 h in sheep and our sampling frequency was once every 15 days.

The decrease in numbers and total diameter of antral follicles ≥3 mm, recorded between 16 and 18 weeks after birth, was previously reported between 16 and 18 weeks after birth in Suffolk × Western White Face ewe lambs using ultrasonography (Bartlewski et al., 2002). Such a decrease in numbers of vesicular follicles has also been reported in fine-wool Merino ewe lambs at 12 weeks after birth (Kennedy et al., 1974). It seems that this decrease is a real effect. It may be explained by the loss of developing follicles by obturation-type atresia and the presence of atretic follicular scars in histological sections of ovaries at 16 weeks of age and the decrease in LH levels. Therefore, LH did not reach the threshold necessary for follicles to continue growing. Indeed, a specific LH threshold for different stages of follicle development is required (Wu et al., 2000). A recent study on ovary mice found that LH-R knockout resulted in abnormal antral follicles containing degenerating oocytes (Zhang et al., 2001) and reduced aromatase activity was associated with atresia (Carson et al., 1981; Tsonis et al., 1984).

There is less information on variations in gonadotropin hormones in relation to follicle development from birth to puberty in other breeds of sheep. In a previous study (Tassel et al., 1978) on gonadotrophin levels and ovarian development from birth to 10 weeks of age in Merino lambs ewes, plasma FSH increased between two and eight weeks of age. The number of vesicular follicles ≥1 mm in diameter increased from birth to four weeks of age, and showed two peaks at four and eight weeks. The size of large follicles increased between two and six weeks of age. LH levels remained low and were relatively stable throughout the experiment. However, small peaks were seen in individual animals from two weeks of age onwards. However, the study found no relationship between fluctuations in gonadotropin levels and variations in number and size of growing and vesicular follicles because all growing and vesicular follicles greater and less than 1 mm in diameter were counted. However, the increased number of vesicular follicles and
increased plasma FSH, but not LH, was in agreement with the present study. Moreover, other studies have also shown variations in levels of LH in female lambs during this period of life. An increase in LH, approximating that of adults, was found at nine weeks of age in ewes (Foster et al., 1975b), indicating adequate pituitary LH for ovulation (Liefer et al., 1972). Other reports indicated that during the first six weeks after birth, concentrations of circulating luteinizing hormone, measured daily, were much greater and more variable than baseline levels found in adults (Foster et al., 1972; Liefer et al., 1972). In an earlier study in fall-born Bulgarian sheep, peripheral plasma FSH and LH increased significantly after 10 days of age (Georgieva et al., 1994), but in Merino (Tassel et al., 1987; Tassel et al., 1976) and in Shropshire ewe lambs (Foster et al., 1975a), levels did not vary significantly from birth to 10 weeks of age. Another study showed a marked increase in serum LH between birth and 18 days (Foster et al., 1972). These studies did not investigate the pattern of follicular growth. The present study in Ouled Djellel ewe lambs showed an increase in both FSH and LH from birth to 10 weeks of age. It seems there was an increase in secretion of LH during the early life of sheep.

Results from various studies on follicle development in ewe lambs suggest that the number of antral follicles is high but variable at birth (Mansour, 1959; Land, 1970; Kennedy et al., 1974; Tassel et al., 1978) and that the increase varied during postnatal development in sheep. An increase in the number of follicles from birth to eight weeks was seen; then a decline to relatively stable numbers until first ovulation (Kennedy et al., 1974). Another study reported that the number of antral follicles in the ovary of 12-weeks-old lambs of the Romanov and Ile-de-France breeds, was higher than that seen in sexually mature animals (Driancourt, 1986). Other studies found abundant vesicular follicles at four weeks after birth, while the diameter of the largest follicle in the ovaries of prepubertal ewe lambs increased to 12 weeks of age and then showed no further change (Kennedy et al., 1974). Bartlewski et al. (2002) showed that the number and total diameter of all follicles <3 mm in diameter increased from 14 to 16 weeks, decreased between 16 and 18 weeks, and then rose again between 22 and 24 weeks after birth and the diameter of the largest follicle increased significantly from 8 to 16 weeks of age and subsequently increased between 22 and 24 weeks of age before the first ovulation.

5. Conclusion

The pattern for plasma FSH and LH levels in Ouled Djellel ewe lambs during postnatal development differs from those reported in the literature for other breeds. It may be breed-specificity; however, it is difficult to make this claim on the evidence presented here.

Two or three peaks in plasma FSH and LH levels preceded puberty and first ovulation in this breed and first ovulation occurred around 24 to 26 weeks of age. The increase in follicle numbers and size generally reflected the pattern of plasma FSH and LH levels.

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