



## Concentrations of Progesterone and Estradiol in Peripheral Plasma during the Estrous Cycle and after Ovariectomy in Huanghuai Goats of High or Poor Prolificacy\*

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**ABSTRACT :** The objective of this study was to characterize the litter sizes in Huanghuai goats with high prolificacy (HP, five or more kids born per litter on at least one occasion), and to compare their peripheral blood concentrations of progesterone and estradiol with those of goats with poor prolificacy (PP, up to three kids born per litter on any occasion). The circulating concentrations of progesterone and estradiol were measured by radioimmunoassay from daily blood samples taken during natural estrus cycles and at 1-5 days after ovariectomy. Estrus was synchronized using two doses of a prostaglandin analog. Litter size for the HP goats increased up to a parity of five and decreased thereafter. The percentage of goats with litter sizes of  $\geq 4$  from parities 3 to 6 ranged from 44.5% to 58.3%. Although small differences in litter size were obtained for goats of parities three, four and six relative to five, parity five does had the highest mean litter size. Progesterone concentrations began to rise earlier and were higher in the HP than in the PP goats on most days of the luteal phase, but not during the follicular phase of the cycle or after ovariectomy. There was a significant difference between the two groups ( $p < 0.05$ ) in the magnitude of the progesterone plateau. Mean estradiol concentrations in the HP group remained significantly higher than in the PP group ( $p < 0.05$ ) during the estrus cycle. There were two estradiol peaks in the HP goats during the early luteal phase, but only one in the PP group. Measurements of individual corpora lutea (CL) *in vitro* showed that there was a greater prevalence of small CL ( $< 6$  mm in diameter) in the HP group than in the PP group ( $p < 0.05$ ). After ovariectomy, the estradiol level on day 1 was significantly higher than at the nadir during the estrus cycle in both the HP ( $p < 0.01$ ) and PP ( $p < 0.05$ ) goats, while levels decreased by 12.3% and 26.2% respectively compared with the mid-luteal period in HP and PP goats ( $p < 0.05$ ). The overall mean estradiol concentrations in HP goats were lower than in the PP group, but no significant differences were found between groups at 1-5 days after ovariectomy. (**Key Words :** Huanghuai Goat, Prolificacy, Progesterone, Estradiol, Estrous Cycle)

### INTRODUCTION

Regulation of the number of ova shed and hence litter size is crucial to successful reproduction in all mammals (Baird and Campbell, 1998). Mechanisms of prolificacy are likely to involve reproductive endocrine factors and genes that have been conserved throughout evolution. In small ruminants, prolificacy is determined essentially by ovulation rate and this in turn is determined by preovulatory

ovarian follicular development. Although the central role of gonadotropins in follicular growth, development and ovulation has been well established, it has become increasingly apparent that other endocrine factors have important ancillary roles in these processes (Nett et al., 2002). The blood plasma concentrations of progesterone play an important role in the control of follicular turnover. This effect is most probably mediated by luteinizing hormone (LH) pulsatility, as has been postulated for cattle (Savio et al., 1993a). High progesterone concentrations lead to lower levels of stimulation of the developing follicles by reducing pulsatile LH secretion (Mann et al., 1992; de Castro et al., 1999; Edgardo et al., 2003). There is good evidence that the estradiol produced mainly by the largest member of the follicular wave is correlated negatively with follicle stimulating hormone (FSH) concentrations during the early luteal and follicular phases (Palta et al., 1998; Gibbons et al., 1999; Violes et al., 2002). Progesterogens

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and estrogens are also secreted by the adrenal gland (Shaikh and Shaikh, 1975; Adams et al., 1990). A clear understanding of the steroid hormone changes associated with prolificacy would seem to be essential to make full use of ovariectomized ewes as a model for studies on the changes in progestogens and estradiol arising from non-gonadal sources. However, very little is known about the adrenal steroid metabolism of prolific goats.

In goats, the presence of two or more large follicles in each wave of ovarian follicular development could be explained by the concept of co-dominance (Rubianes and Menchaca, 2003; Cueto et al., 2006). However, compared with the literature for sheep, there is little information about differences in the patterns of secretion of pituitary gonadotropins or ovarian hormones between goats of different prolificacy. It is known that the *FecB* gene acts at the ovary to enhance ovarian sensitivity to gonadotropin stimulation (Souza et al., 1997; Campbell et al., 2003). Moreover, there are no differences in peripheral concentrations of estradiol during the follicular or luteal phase between Merino ewes with and without the Booroola *FecB* gene for fecundity (Scaramuzzi et al., 1983; Souza et al., 1997a; Campbell et al., 2003). However, the available evidence indicates that the patterns of secretion of pituitary gonadotropins or ovarian hormones in goats are not identical to those in ewes (Rawlings et al., 2003).

Huanghuai goats are not seasonal breeders and are considered one of the most important local breeds in China as they are highly prolific and have good leather and meat production potential. The number of kids born per goat averages 2.38, but the prolificacy of the goats is somewhat irregular (Zhao et al., 2005). Some very highly prolific does sometimes have only one lamb born. This complex trait involves a combination of ovulation rate, embryo viability and uterine capacity in swine (Bennett and Leymaster, 1989). To date, mechanisms controlling prolificacy in goats are unclear. Therefore, the primary objective of this study

was to investigate the trait of prolificacy and to characterize differences in ovarian hormone levels of prolific and non-prolific goats throughout natural estrus cycles. We examined the litter sizes of Huanghuai goats, and analyzed hormonal profiles (estradiol and progesterone) during natural estrus cycles synchronized using a prostaglandin analog and at five days after ovariectomy.

## MATERIALS AND METHODS

### General

Huanghuai goats are mostly distributed in the Huanghuai plain with considerable annual rainfall (741-1,000 mm) and moderate average air temperatures (13-16°C). Domestication and artificial selection have led to high prolificacy in this goat breed (Zhao et al., 2005). The goats are maintained on dry, natural pasture and are supplemented with grain *ad libitum*. Ewes are first exposed to bucks at approximately eight months of age. The common mating system is three lambings every two years.

### Experimental design

*Experiment 1*: To characterize litter size in the highly prolific goats each year, the date of lambing and number of kids born were recorded in 6,450 goats including 427 highly prolific does. Table 1 lists these goats, kept in 398 flocks in 2004. These flocks were distributed in the Jianghuai area of China and have been monitored since 1997.

*Experiment 2*: To determine differences in progesterone and estradiol levels between HP and PP goats, two sequential natural estrous cycles of two groups of goats, either with high prolificacy (HP,  $\geq 5$  kids born per litter on at least one occasion,  $n = 4$ ) or with poor prolificacy (PP,  $\leq 3$  kids born per litter on any occasion,  $n = 4$ ) were studied. Initial estrus synchronization was achieved using two intramuscular injections of 0.1 mg of a synthetic analog of prostaglandin F2 alpha (Estrumate; Ningbo Sansheng

**Table 1.** Litter sizes among goats with high prolificacy

Parity	<i>n</i>	Mean litter size	Goats with litter size $\geq 4$ (%)	Minimum litter size (% goats)	Maximum litter size (% goats)
1	427	2.53 $\pm$ 0.05 <sup>D</sup>	17.80 <sup>G</sup>	1(10.77)	7(0.23)
2	427	3.13 $\pm$ 0.05 <sup>C</sup>	27.87 <sup>F</sup>	1(4.22)	7(0.23)
3	427	3.56 $\pm$ 0.06 <sup>B</sup>	44.50 <sup>Cd</sup>	1(0.47)	6(3.51)
4	423	3.66 $\pm$ 0.06 <sup>B</sup>	53.66 <sup>AB</sup>	1(3.78)	7(0.24)
5	400	3.78 $\pm$ 0.06 <sup>A</sup>	58.25 <sup>A</sup>	1(2.75)	7(0.50)
6	310	3.60 $\pm$ 0.08 <sup>B</sup>	47.42 <sup>BC</sup>	1(3.23)	7(0.97)
7	243	3.26 $\pm$ 0.08 <sup>C</sup>	37.45 <sup>DE</sup>	1(4.12)	7(0.82)
8	203	3.13 $\pm$ 0.10 <sup>C</sup>	34.98 <sup>Ef</sup>	1(9.85)	7(1.48)
Total	427	3.33 $\pm$ 0.02	40.24	1(4.65)	7(0.45)

Values sharing the same capital or lowercase letters are not significantly different. Values with the same letters in which one is capital and the other is lowercase are significantly different at  $p < 0.05$ . Values with different letters between them are significantly different at  $p < 0.01$ .

Pharmaceutical Co. Ltd., China) given 12 d apart. The goats were ovariectomized on day 9 after the onset of the fourth estrus to measure the diameters of corpora lutea (CL) in the ovaries and to determine differences in progesterone and estradiol levels between the groups.

The animals were 3-5 years old, non-lactating and of parity 4-5, from the breeding station of Ao-Hua Co. in Xu-Zhou of Jiangsu Province. During the experimental periods, the does were restrained loosely by being tied to stanchions outdoors and were allowed free access to food and water. Estrous behavior was checked twice daily with an aproned mature teaser buck and was confirmed when the doe stood to be mounted. The experiment was conducted from September to December, 2007.

Jugular blood samples (2 ml) were collected once daily from day 1 of the natural estrus to day 5 after ovariectomy into heparinized vacutainer tubes via indwelling jugular catheters (vinyl tubing; 1.00 mm i.d.×1.50 mm o.d.; Biocorp Australia Proprietary Ltd., Australia). Cannulae were inserted 24 h before the first bleed and were filled with heparinized saline between bleeds (250 IU of heparin sodium per milliliter of isotonic saline; Hepalean, Organon Teknika Inc., Canada). Samples were taken at 12-minute intervals for 3.2 h over 2-3 days before estrus (proestrus, PET), on days 11-12 after estrus (mid-luteal phase, MLP), and for 2.6 h on days 1 (FRDOR) and 5 after ovariectomy (FFDOR). Plasma was obtained after centrifugation for 20 min at 4,000 g and stored at -20°C until it was assayed for progesterone and estradiol.

#### Hormone analysis

Plasma concentrations of estradiol-17 $\beta$  and progesterone were determined by double-antibody radioimmunoassay using <sup>125</sup>I-labeled radioligands as described by Meikle et al. (1997) and using antisera against estradiol-17 $\beta$  (GDN 244) and progesterone (GDN 337) (Beijing Furui Bioengineering Co., China). The respective intra- and inter-assay coefficients of variation were 5.7% and 7.4% for estradiol-17 $\beta$  and 8.8% and 12.1% for progesterone.

#### Statistical analysis

The serially intensive samples of individuals were analysed for estradiol pulses during PET, MLP, FRDOR and FFDOR, basically as described by Merriam et al. (1982). The nadirs were calculated for each profile and were used in the analysis of group effects. The concentrations of progesterone and estradiol across the estrous cycle and five days after ovariectomy and between HP and PP goats were analyzed by repeated samples ANOVA and as fitted to a generalized linear mixed model, using SPSS version 13.0 (SPSS Inc., Chicago, IL, USA), with systematic effects of group and time, random effects of animals, and an animal-

by-time interaction. Comparison of the litter sizes between parities was performed by repeated samples ANOVA using the same software. The total CL counts and numbers of Type I (>6 mm) and Type II CL (<6 mm; Dukelow et al., 1971; Scaramuzzi et al., 1981) were evaluated using Chi squared tests.

## RESULTS

#### Litter size

Data on the litter sizes in the HP goats are presented in Table 1. Litter size increased up to parity 5 and decreased thereafter. At all parity levels, parity 5 HP does had the highest mean litter size ( $p<0.01$ ) and parity 1 goats had the smallest ( $p<0.01$ ). However, the average litter size at parity 2 was similar to those at parities 7 and 8. No significant difference was found in mean litter size among the HP goats at parities 3, 4 and 6. As litter size increased from parities 1 to 5, the percentage of goats with  $\geq 4$  kids born per litter increased from 17.8% to 58.3% ( $p<0.01$ ), then decreased to 20.8% ( $p<0.01$ ) at parities 5 to 7. The percentage of goats with litter sizes of  $\geq 4$  from parities 3 to 6 ranged from 44.5% to 58.3%, providing a convenient model to study the reproductive endocrinology of prolificacy. Minimum litter size (1) and maximum litter size (7) were found at all parities, but the overall percentage of goats with these extreme litter sizes was 4.7% and 0.5%, respectively.

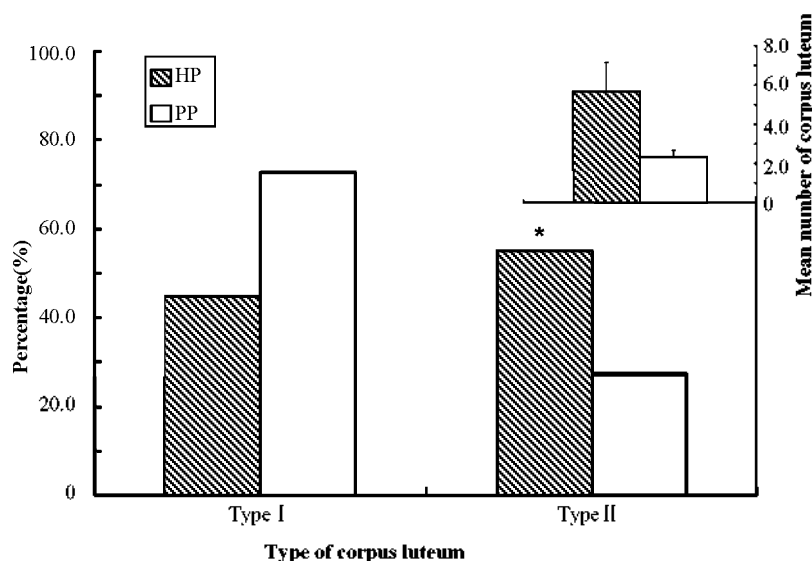
#### Corpora lutea counts

The goats produced both Type I and Type II CL on the same ovary during a single cycle. Figure 1 illustrates the mean numbers of CL and percentages of Type I and Type II CL on day 9 of estrous cycles in the PP and HP does. The mean total number of CL in the HP does was  $5.67\pm 1.45$ , more than in the PP group ( $2.33\pm 0.33$ ,  $p>0.05$ ). Type II CL tended to be more prevalent in the HP group than in the PP group (55.0% versus 27.3%, respectively,  $p<0.05$ ).

#### Patterns of progesterone secretion

Progesterone and estradiol were secreted in a pulsatile manner, which involved the recurrence of obvious peaks followed by nadirs of hormone secretion. These were measured by analyzing representative plasma estradiol and progesterone profiles obtained from frequent blood sampling during days 11-12 of the estrous cycle, 2-3 days before estrus and on the first and fifth day after ovariectomy. The mean plasma progesterone and estradiol concentration profiles of estrus cycles are depicted in Figure 2 and 3.

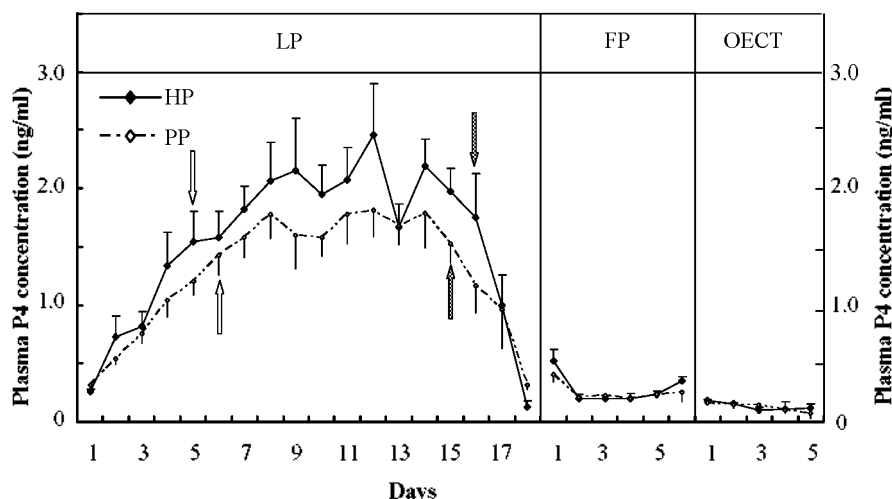
Plasma progesterone levels started to increase from days 1 to 5 after ovulation by 492.3% for the HP group ( $p<0.01$ ) and to day 6 by 361.2% for the PP group ( $p<0.01$ ) (Figure 2, left panel). There were significant differences in concentrations for the HP goats between days 4 and 12 in



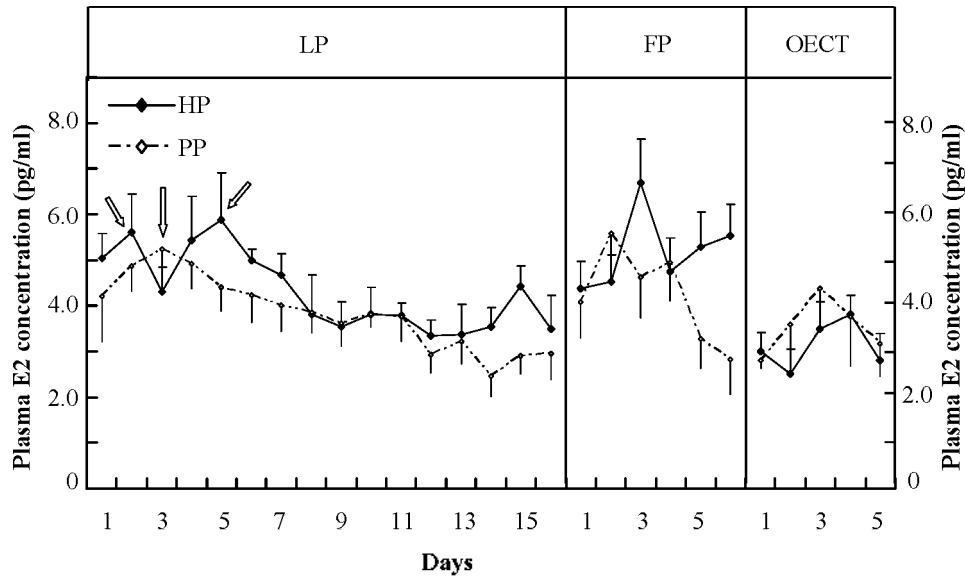
**Figure 1.** Percentages of type I and type II corpus luteum (CL, main graph) and numbers of CL (inset) in the ovaries between highly prolific (HP) and poorly prolific (PP) goats on day 9 of the estrous cycle. Each column and vertical bar represents the mean and SEM (*n* = 4), respectively. For comparisons between groups with the same type of CL, \* *p*<0.05.

the luteal phases ( $1.34 \pm 0.26$  versus  $2.46 \pm 0.44$  ng/ml, respectively; *p*<0.05) and for the PP goats between days 5 and 9 ( $1.20 \pm 0.11$  versus  $1.60 \pm 0.29$  ng/ml, respectively; *p*<0.05). Progesterone plateaued from days 5 ( $1.54 \pm 0.26$  ng/ml) to 16 of the estrus cycle ( $1.75 \pm 0.38$  ng/ml) for the HP group, and from days 6 ( $1.43 \pm 0.17$  ng/ml) to 15 ( $1.53 \pm 0.17$  ng/ml) for the PP goats. Progesterone levels did not differ significantly among the plateaued days but the values decreased rapidly on days 15 and 16. The overall mean progesterone concentrations in the HP goats were not

significantly higher than in the PP goats during the luteal phase ( $1.56 \pm 0.09$  versus  $1.26 \pm 0.06$  ng/ml, respectively), but a significant difference was found between the two groups in the magnitude of the progesterone plateau ( $1.96 \pm 0.09$  versus  $1.65 \pm 0.06$  ng/ml, respectively; *p*<0.01). Plasma progesterone levels remained low during the follicular phase (Figure 2, middle panel) and 1-5 days after ovariectomy (Figure 2, right panel), and no difference was found between the two groups of goats during these periods. These data were also confirmed by the representative



**Figure 2.** Secretory profiles of daily progesterone (P4) in highly prolific (HP) and poorly prolific (PP) female goats during the luteal phase (LP, left panel) and follicular phase (FP, middle panel) and during 1-5 days after ovariectomy (OECT, right panels). Each square and vertical bar represents the mean and SEM, respectively. Open arrows indicate the first day on which the P4 concentration did not differ significantly among the sequential stages in the pre- and mid-luteal phase of each group. Shaded arrows indicate the first day on which P4 decreased significantly (*p*<0.05) in the post-luteal phase.



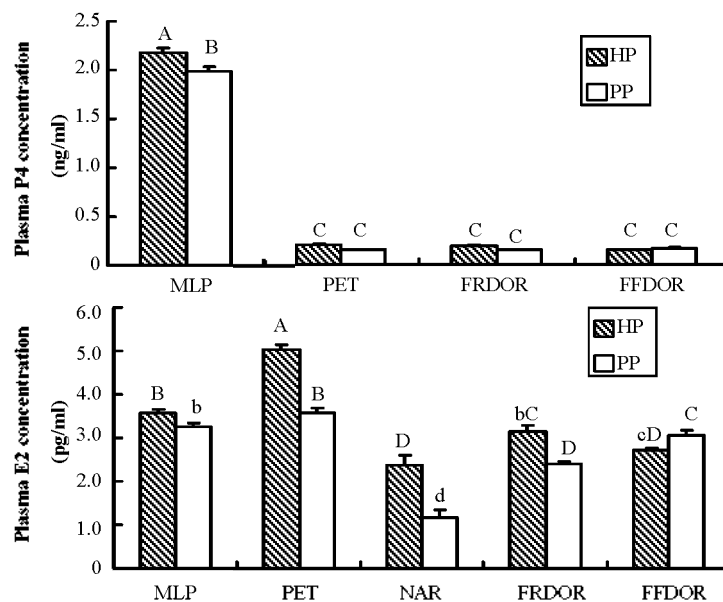
**Figure 3.** Daily estradiol (E2) secretory profiles in highly prolific (HP) and poorly prolific (PP) goats during the luteal phase (LP, left panel) and follicular phase (FP, middle panel) and on 1-5 days after ovariectomy (OECT, right panel). Each square and vertical bar represents the mean and SEM, respectively. Open arrows indicate the peak of estradiol during the early luteal phase.

plasma progesterone profiles obtained from frequent blood sampling in goats during the MLP, PET, FRDOR and FFDOR periods (Figure 4). The fall in value of progesterone from MLP to PET was significantly different between HP and PP groups ( $1.97 \pm 0.19$  versus  $1.84 \pm 0.16$  ng/ml;  $p < 0.05$ ). The duration of the luteal phase in the HP

group was similar to that in the PP group ( $17.00 \pm 0.63$  versus  $17.13 \pm 0.40$  days respectively;  $p < 0.05$ ).

**Patterns of estradiol secretion**

The mean plasma estradiol concentration profiles are depicted in Figure 3 and 4. Plasma estradiol concentrations



**Figure 4.** Plasma progesterone (P4) and estradiol (E2) concentrations obtained from frequent blood sampling in goats during days 11-12 of the estrous cycle (mid-luteal phase, MLP), 2-3 days before estrus (proestrus, PET) and the first (FRDOR) and fifth day after ovariectomy (FFDOR). HP, highly prolific goats; PP, poorly prolific goats; NAR, nadirs of estradiol secretion during estrous cycle. Each column and vertical bar represents the mean and SEM ( $n = 4$ ), respectively. Values sharing the same capital or lowercase letters are not significantly different. Values with the same letters in which one is capital and the other is lowercase are significantly different at  $p < 0.05$ . Values with different letters between them are significantly different at  $p < 0.01$ .

decreased on about day 6 of the estrus cycle and remained low from days 7-15 compared with the pre-luteal (Figure 3, left panel) and follicular phases (Figure 3, middle panel). The overall mean estradiol concentrations in HP goats were generally higher than in the PP group during the estrus cycle. There were significant differences in concentrations between the HP and PP does in the luteal ( $4.39 \pm 0.57$  pg/ml in HP versus  $3.84 \pm 0.54$  pg/ml in PP,  $p < 0.05$ ) and follicular phases ( $5.19 \pm 0.71$  pg/ml in HP versus  $4.22 \pm 0.78$  pg/ml in PP,  $p < 0.05$ ). These results were confirmed by the representative plasma estradiol profiles obtained from frequent blood sampling during the MLP and PET periods (Figure 4). There were two peaks of estradiol in the HP group during the early luteal period ( $5.45 \pm 0.82$  pg/ml on day 2 and  $5.75 \pm 0.92$  pg/ml on day 5) but only one in the PP goats ( $5.24 \pm 0.77$  pg/ml on day 3). The magnitude of the estradiol level measured on days 2, 4 and 5 in HP goats was significantly higher than on days 12 and 13 ( $3.34 \pm 0.36$  and  $3.37 \pm 0.66$  pg/ml, respectively;  $p < 0.05$ ) and the concentration on day 5 was also higher than on day 3 ( $3.84 \pm 0.60$  pg/ml;  $p < 0.01$ ). A significant difference in the estradiol level was found between days 3 and 13 in the PP goats ( $2.92 \pm 0.38$  pg/ml;  $p < 0.01$ ), 14 ( $3.23 \pm 0.50$  pg/ml;  $p < 0.05$ ), 15 ( $2.45 \pm 0.44$  pg/ml;  $p < 0.01$ ), and the estradiol concentrations on days 2 ( $4.88 \pm 1.58$  pg/ml) and 4 ( $4.92 \pm 0.55$  pg/ml) were higher than on days 13 and 15 ( $p < 0.05$ ,  $p < 0.01$ , respectively). After ovariectomy, the estradiol concentrations were significantly higher ( $p < 0.01$ ) in the HP than in the PP goats during FRDOR, but this pattern reversed to be significantly lower ( $p < 0.05$ ) during FFDOR. Thus, although the overall mean estradiol concentrations in HP goats were lower than in the PP group, no significant differences were found during 1-5 days after ovariectomy. There were significant differences in estradiol concentrations between the mid-luteal period and the ovariectomized phase in the HP and PP groups ( $p < 0.05$  for both). The estradiol levels on day 1 after ovariectomy were significantly higher than during the nadirs of the estrus cycle in the HP goats ( $3.13 \pm 0.17$  pg/ml versus  $2.37 \pm 0.22$  pg/ml,  $p < 0.01$ ), and in the PP group ( $2.40 \pm 0.08$  pg/ml versus  $1.71 \pm 0.17$  pg/ml,  $p < 0.05$ ). The estradiol concentration at this point decreased by 12.3% and 26.2% in HP and PP goats, respectively, compared with the mid-luteal period ( $p < 0.05$ ).

## DISCUSSION

The litter size for the highly prolific goats in this study increased with successive pregnancies until they reached parity 5, and decreased thereafter. Although small differences in litter size were obtained for goats of parities 3, 4 and 6 relative to 5, parity 5 does had the highest mean

litter size. Furthermore, goats at these parity stages also had noticeably higher performance with four or more kids born per litter outside this range, as has been reported for sheep (Shelton and Menzies, 1968; Waldron and Thomas, 1992). Using this concept, the total numbers of CL in the HP does in this study were more than in the PP group, indicating that ovulation rate must be the upper limiting factor for goats with low litter sizes, as is seen in sows (Bennett and Leymaster, 1989; Tantasuparuk and Techakumphu, 2005). However, 10.8% of goats had only one kid born in the first pregnancy, an observation that has led to suggestions that both litter size and ovulation rate are positively correlated with doe body weight (Young et al., 1963; Waldron and Thomas, 1992). The present results support this conclusion for body weight, as in this mating system the females were first exposed to males at about 70% of their adult body weight.

We present here the first report of plasma profiles of progesterone and estradiol in highly prolific Huanghuai goats compared with nonprolific females across the estrous cycle and after ovariectomy. Plasma progesterone concentrations did not differ significantly between HP and PP does during the follicular phase. However, on most of the days during the luteal phase the progesterone concentrations were higher in the HP than in the PP groups. These data are similar to observations in Merino ewes homozygous for the Booroola *FecB* fecundity gene (Xia and O'Shea, 2003). In the present study, a characteristic feature of HP goats was that their ovaries had higher numbers of the smaller CL than did the PP does. The early increase in progesterone during the luteal phase might result at least in part from the earlier development of the CL pool. The high concentrations of progesterone seen in the plateau phase in HP goats relative to PP were also physiologically relevant, in that they reflected the pooled output from many small CL, similar to the tendency observed in Booroola ewes (Souza and Campbell, 1997a). Thus, the falling progesterone levels in the plateau and early follicular phases, which are involved with inducing the pre-ovulatory surge of gonadotropins (Nett et al., 2002), were greater in the HP than the PP goats, an observation which has led to suggestions that this large decrease might be related to high ovulation rate. These data are in agreement with those for Booroola ewes (Bindon et al., 1981; McNatty et al., 1986; Niswender et al., 1990; Xia and O'Shea, 2003). It is well known that the *FecB* gene of prolific ewes plays a key role in ovulation. However, the mechanism behind the high prolificacy of these goats remains unclear.

The increased secretion of estradiol is normally associated with the development of waves of follicular growth (Mann et al., 1992; Souza et al., 1997; de Castro et al., 1999). We observed two estradiol peaks in the HP group

during the early luteal phase, but only one in the PP group, presumably reflecting a difference in the pattern of waves of follicular growth between these groups. The first estradiol peak emerged earlier and also declined earlier in the HP than in the PP goats, and progesterone concentrations in HP exceeded those found in the PP does during the same period. These findings are consistent with studies on the relationship between progesterone concentrations and the numbers of follicular waves (de Castro et al., 1999; Menchaca et al., 2002). Namely, high progesterone concentrations probably decrease LH pulsatility and the early decrease of estradiol allows an early rebound of FSH concentrations, promoting the emergence of the second follicular wave. Thereafter, the emergence of the subsequent wave is also advanced. The present study has demonstrated the existence of an acceleration of follicular turnover in HP goats. This is in agreement with pharmacological studies performed in the cow (Adams et al., 1992) and the ewe (Rubianes et al., 1996) and scanning observations of Menchaca et al. (2002) on goats.

The mean size of the CL pool in the ovary is usually correlated with pre-ovulatory follicular size in goats (Camp et al., 1983; de Castro et al., 1999). In the present experiment using measurements of individual CLs, there were more CLs designated type II in the HP goats than the PP goats. Thus the HP goats produced more small preovulatory follicles than the PP animals, as previously demonstrated in Booroola ewes (McNatty et al., 1986; Souza et al., 1994). Furthermore, goats with high progesterone concentrations tend to have smaller follicles than those developing when progesterone concentrations are low (Ginther and Kot, 1994; de Castro et al., 1999; Menchaca and Rubianes, 2002). Therefore, based on these differences in progesterone concentrations between low and high fecundity groups, our data also suggest that there are more follicles present during subsequent waves of follicular development in the estrus cycle among HP goats and that they mature at a smaller size than those in PP animals.

During this experiment, major differences were observed before and after ovariectomy, which could not be accounted for by the changes in ovarian follicles. The estradiol levels on day 1 after ovariectomy were significantly higher than the nadirs observed during normal estrus cycles, which decreased by 12.3% and 26.2% in HP and PP goats respectively, compared with the mid-luteal period. Our results suggest that the ovaries are not a unique source of circulating surges of estradiol. This has also been noted in women and rats (Shaikh and Shaikh, 1975; Ellison, 1984). It seems likely that estradiol from non-gonadal sources might play a role in regulation of the hypothalamic-pituitary axis, reproductive system and estrus cycle of goats,

as previously demonstrated in sheep (Martin, 1983; Adams, et al., 1990; Joseph et al., 1992). However, further research is required to test this hypothesis for goats and to study the role of non-gonadal hormones in reproduction in HP goats.

In the present study, mean estradiol concentrations remained higher in the HP group during the estrus cycle than in the PP does. This is different from Booroola ewes in which there are no differences in the patterns of estradiol secretion between ewes of different prolificacy (Scaramuzzi et al., 1983; McNatty et al., 1986; Montgomery et al., 1992; Souza et al., 1997). Therefore, further studies are necessary to explore the nature of the estradiol negative feedback mechanisms regulating the secretion of FSH and the hypothalamic GnRH regulatory system if we are to understand the hormonal control of ovarian function among HP goats.

In summary, the litter size for these highly prolific Huanghuai goats increased with successive pregnancies until they reached a parity of 5, and decreased thereafter. The pre-ovulatory follicles and CL were smaller but more prevalent in goats of high prolificacy, resulting in different secretion patterns of progesterone and estradiol compared with poorly prolific does. Mean concentrations of progesterone in the highly prolific goats increased more quickly during the early luteal phase and the estradiol concentrations remained higher during the estrus cycle, compared with goats of poor prolificacy. The ovaries are not a unique source of circulating surges of estradiol in prolific goats.

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