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Expression of Progesterone Receptor Membrane Component 1 (*PGRMC1*) in Follicular and Luteal Tissues in Goats – Effect of Short-term Concentrate Supplementation

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ABSTRACT

This study evaluated the effects of short-term supplementation with concentrate on ovulation rate, plasma progesterone concentrations and gene expression for Progesterone Receptor Membrane Component 1 (*PGRMC1*) in ovarian tissues of Boer goats. Twenty females were allocated to two groups: 1) Control, receiving a maintenance diet consisting of 70% Napier grass plus 30% concentrate (4.45 MJ/day); 2) Supplemented, receiving twice their required metabolizable energy for maintenance by adding extra concentrate (8.90 MJ/day). The dietary treatments were applied for 25 days, beginning 5 days before (Day 5) CIDR removal (Day 0). On Day 19, the ovulation rate was estimated by trans-rectal ultrasonographic scanning. Blood was sampled for progesterone (P4) analysis every 2 days, from Days 9 to 27. On Day 27, the level of expression of *PGRMC1* was assessed in follicles and corpora lutea. The ovulation rate was not affected by treatment (Control 1.00 ± 0.24; Supplemented 1.25 ± 0.25). Over Days 13 to 27, plasma P4 concentrations were significantly ($p<0.05$) greater in the Supplemented group than in the Control group. The expression of *PGRMC1* in follicular and luteal tissues was greater in the Supplemented group than in the Control group ($p<0.05$). There was a positive correlation between *PGRMC1* expression and P4 concentration ($r= 0.65$, $p<0.05$). It was concluded that, in goats, short-term concentrate supplementation could increase P4 concentrations, at least in part, by influencing the expression of *PGRMC1*. This finding suggests that short-term concentrate supplementation can support embryo development during the luteal phase and early stages of pregnancy.

Keywords: goat; nutritional supplement; ovulation rate; PGRMC1; progesterone

INTRODUCTION

Commercial concentrate has been used as a supplement for ruminants in many countries, including some in Asia (Widiani *et al*., 2020; McKay *et al*., 2019; Worku *et al*., 2020). According to Norhazirah *et al.* (2016), who conducted a survey on goat production systems in Peninsular Malaysia, about 83% of farmers provide their goats with commercial concentrate, and of that percentage, 42% offered additional concentrate to improve the kidding rate.

In sheep, increased energy intake significantly influences the growth of dominant follicles and can increase ovulation rates through metabolic and neuroendocrine signals (Banchero *et al*., 2020; Juengel *et al*., 2021). However, studies in goats show that while energy level can affect pituitary hormone secretion, it does not consistently improve ovulation rate (Haruna *et al*., 2009). Moreover, a study by Nogueira *et al.* (2016) found that although nutritional supplementation increased plasma concentrations of insulin, leptin, and IGF-1, factors involved in the modulation of folliculogenesis in ruminants (Juengel *et al*., 2021), there was no consistent translation to increased ovulation rates – rather, ovulation rate was more effectively influenced by exogenous hormones.

A potential problem with nutrition supplements is that the benefit of an increase in ovulation rate might be offset by a reduction in circulating progesterone concentration, contributing to early embryo loss, thus diminishing the contribution of higher ovulation rate to litter size (Parr *et al*., 1993; Robertson *et al*., 2015), although this same process might not apply to goats (Shikh Maidin *et al*., 2014). Unlike sheep, where progesterone is initially produced by the corpus luteum (CL) and later by the uterus, goats rely solely on the CL for progesterone throughout pregnancy, making sustained CL function crucial for fetal development

(Kandiel *et al*., 2010), so we could expect different relationships between nutrition, progesterone and embryo survival.

Nutrition is known to influence progesterone production by affecting the expression of genes related to progesterone signaling. For example, in cows, dietary supplementation with conjugated linoleic acid (CLA) increases plasma progesterone concentrations and alters gene expression related to the endocannabinoid system in the endometrium (Abolghasemi *et al*., 2016). In sheep, nutrition can also alter the dynamics of *PGR* expression, especially during the luteal phase (Grazul-Bilska *et al*., 2018). Progesterone receptor membrane component 1 (*PGRMC1*) works alongside membrane progestin receptors (*mPRs*) to mediate non-genomic, rapid actions of progesterone. *PGRMC1* is implicated in various reproductive tissues, playing roles in the anti-mitotic and anti-apoptotic effects of progesterone in granulosa cells of the follicle (Peluso & Pru, 2014; Yuan *et al*., 2018), CL function and progesterone signaling (Kowalik *et al*., 2014). Variations in *PGRMC1* expression across the estrous cycle suggest its potential role in mediating nutritional effects on CL function and progesterone levels (Kowalik *et al*., 2014).

Currently, there is a significant knowledge gap regarding *PGRMC1* expression in the follicular and luteal tissues of goats, and there has been little research into whether nutrition affects *PGRMC1* expression in these reproductive tissues or progesterone secretion. Using Boer goats, the present study tested whether short-term concentrate supplementation will enhance ovulation rate, upregulate PGRMC1 expression in follicular and luteal tissues, and increase circulating progesterone concentrations, thereby improving reproductive outcomes of female Boer goats.

MATERIALS AND METHODS

Experimental Design

The experimental procedures were approved by The Institutional Animal Care and Use Committee (IACUC) of Universiti Putra Malaysia (Reference: UPM/IACUC/AUP-R064/2016).

We used 20 female Boer goats, aged between 2 and 3 years, with an average live body weight of 27.0 ± 0.9 kg and body condition score (BCS) of 2.3 ± 0.1. All animals were kept in individual pens (1.5 m x 0.5 m). They were randomly allocated to either the Control group (n= 10), receiving a daily maintenance diet (4.45 MJ/day), or the Supplemented group (n= 10), receiving the same daily maintenance allowance but with sufficient concentrate to supply double their metabolizable energy for maintenance (MEm; 8.90 MJ/day). Water was available *ad libitum*. The maintenance diet comprised 70% Napier grass and 30% commercial concentrates. The amount of feed for each doe in the control group was calculated to meet their MEm and thus ensure the maintenance of their live weight. Table 1 summarises the metabolized energy, crude protein, and dry matter contents of Napier grass and commercial concentrate utilized.

Oestrus cycles were synchronized with an intravaginal device containing 0.3 g progesterone (CIDR, Eazi-Breed® CIDR®, Pfizer Australia) for 18 days, from Days 18 to 0 (the day of CIDR removal). The feeding treatment for the Supplemented group began on Day 5 and lasted 25 days. On Days 2 to 4, the does in both groups were introduced to bucks for natural mating, and on Day 19, the left and right ovaries were observed for the presence of CL by using trans-rectal ultrasound (SSD-900; Aloka, Tokyo, Japan). Ovulation rate was defined as the number of CL per doe. Blood was sampled for progesterone (P4) every 2 days, from Days 9 to 27. All blood samples were centrifuged and the plasma was stored at a temperature of –20 °C until assayed.

On Day 27, all does were slaughtered and both ovaries were immediately excised. Follicles (> 3 mm diameter) and CL were collected from the ovaries and stored in RNALater (Qiagen, USA) at –20 °C until real-time qPCR analysis.

Progesterone Assay

Plasma concentration of P4 was assayed in duplicate by using a progesterone ELISA kit (ENZO Life Sciences Inc., Farmingdale, NY, USA; ADI-901-011) that displayed 100% cross-reactivity with P4. The limit of detection was 8.57 pg/mL. The intra and inter-assay CVs were 7.9% and 6.2%, respectively.

RNA Extraction and cDNA Synthesis

Total RNA was extracted from follicles and CL tissue samples by using the RNeasy mini kit (Qiagen, USA). On-column DNase digestion was performed using RQ1 RNase-Free DNase (Promega, USA) to eliminate genomic DNA contamination. The presence of 28S rRNA and 18S rRNA bands on 1% agarose gel was assessed to ensure the extracted total RNA was intact, followed by confirmation of concentration and purity using NanoVue™ Plus Spectrophotometer. Only samples that were intact and free from protein contamination, with a ratio of OD 260/280 between 1.8 and 1212.0, were utilized. From each sample, 1 μg total RNA was reverse-transcribed into complementary DNA (cDNA) by using Transcriptor First Strand cDNA Synthesis Kit (Roche, USA) and the cDNA was stored at –20 °C until real-time qPCR.

Real-Time Quantitative Polymerase Chain Reaction (RT-qPCR)

Primers used to amplify the goat *PGRMC1* gene were designed on the basis of selected *PGRMC1*

Table 1. Proximate analysis of Napier grass (*Pennisetum purpureum*) and commercial concentrate fed to the does

Type of feed	Nutrient content		
	DM (%)	ME (MJ/kg)	CP (%)
Napier grass	25.10	6.47	3.40
Concentrate	89.57	12.35	15.22

Note: DM= Dry matter; ME= Metabolizable energy; CP= Crude protein.

gene sequences obtained from the National Centre for Biotechnology Information (NCBI). Primers were designed within the exon region of the full-length *PGRMC1* sequences that were aligned using Primer 3 software. Primers that had been used to amplify the glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and B-actin reference genes have been described by Celestino *et al*. (2010); the ubiquitin reference gene was described by Frota *et al.* (2011) (Table 2).

The master mix for the RT-qPCR analysis was prepared by using the KAPA SYBR FAST qPCR kit master mix (2X) universal (KAPA Biosystems, USA). The assay was performed in a LightCycler 480 (Roche, USA). PCR amplification for each sample was performed in a 20 µL final volume containing 7.2 µL nuclease-free water, 10 µL SYBR master mix (1X), 0.4 µL forward primer (200 nM), 0.4 µL reverse 140primer (200 nM) and 2 µL cDNA (100 ng). Nuclease-free water was included as a negative control. The cycling profile included a single cycle of enzyme activation (95 °C for 5 min), followed by 40 cycles of denaturation, annealing, and extension (94 °C for 15 s, 60 °C for 30 s, and 72 °C for 45 s, respectively). All samples were analyzed in triplicate. The relative normalized expression level was calculated by using the Delta-delta-CT (2−ΔΔCt) method (Livak & Schmittgen, 2001). The GAPDH, B-actin, and ubiquitin genes were used as endogenous controls, whereby *PGRMC1* gene was normalized against the average CT values of GADPH, B-actin, and ubiquitin, while the Control group (non-supplemented does) was used as a calibrator group.

Statistical Analysis

Out of the 20 animals sampled, data from three does (1 Control and 2 Supplemented) were excluded from statistical analysis due to abnormal feeding behavior. Statistical analysis was carried out by using SPSS software version 26. The effects on ovulation rate were compared using the Chi-squared test. The effects of dietary treatment on P4 concentration were assessed by repeated-multivariate ANOVA and the data for *PGRMC1* expression was subjected to independent T-test. Spearman rank correlation analysis was used to correlate *PGRMC1* expression and P4 concentration. The *PGRMC1* expression data are presented as fold change ± SD with respect to the control level (arbitrarily set to 1) for relative gene expression. Statistical significance was set at $p<0.05$.

RESULTS

Table 3 shows that neither live body weight nor body condition score differed between treatments at the beginning or at the end of the experimental period. Supplementation did not significantly affect the number or diameter of CL, but it did significantly increase circulating progesterone concentrations as compared to controls ($p<0.05$).

Progesterone concentration was not correlated with the number of CLs (Figure 1), suggesting does with one or two CLs had similar average P4 concentrations within their respective groups. However, P4 concentrations differed significantly between treatment groups. As shown in Figure 1, on Day 19, supplemented does with one CL had greater P4 concentrations than controls (10.3 ± 2.82 ng/mL vs. 7.6 ± 3.37 ng/mL; $p<0.05$). Similarly, on Day 27, supplemented does with two CLs exhibited significantly greater P4 concentrations than control does (14.1 ± 2.41 ng/mL vs. 10.7 ± 2.81 ng/mL; $p<0.05$).

Figure 2 shows plasma P4 concentrations were similar in the two groups from Days 9 to 11, but from day 13 onward, supplemented does consistently exhibited significantly higher P4 levels than controls ($p<0.05$). For example, on Day 13, P4 concentrations in supplemented does averaged 5.69 ng/mL compared to 3.61 ng/mL in controls, and this difference persisted through Day 23. Although P4 levels slightly declined after supplementation ended (Days 23 to 27), the differences between groups remained significant ($p<0.05$).

Table 3. The initial and final values for live body weight and body condition score (BCS) after treatment, as well as the number and diameter of corpora lutea, plasma progesterone concentration on Day 27, in control and supplemented Boer goats

Variables	Treatments	
	Control	Supplemented
Initial live weight (kg)	27.06 ± 0.80	27.01 ± 1.72
Live weight after treatment (kg)	27.61 ± 0.70	28.95 ± 1.50
Initial BCS (units)	2.25 ± 0.10	2.44 ± 0.20
BCS after treatment (units)	2.30 ± 0.10	2.50 ± 0.20
Corpus luteum number (units)	1.3± 0.24	1.9 ± 0.29
Corpus luteum diameter (mm)	0.9 ± 0.10	0.9 ± 0.16
Progesterone (ng/mL)	7.88 ± 0.26[a]	10.77 ± 0.28[b]

Note: Difference superscripts in the same row indicate a significant difference ($p<0.05$).

Table 2. Primers used in real-time quantitative polymerase chain reaction (RT-qPCR)

Gene	Primer sequence (5′→3′)	Amplicon size (bp)	Accession no./ Reference
PGRMC1 (Target)	F: CCTGAGAGACGGGTAAAACAT R: GTCCCCAAACAGAGAAAGTAGG	297	XM013976238.1
B-actin (Housekeeping)	F: ACCACTGGCATTGTCATGGACTCT R: TCCTTGATGTCACGGACGATTTCC	200	AF481159/ Celestino *et al.* (2010)
GADPH (Housekeeping)	F: TGTTTGTGATGGGCGTGAACCA R: ATGGCGTGGACAGTGGTCATAA	154	AJ431207/ Celestino *et al.* (2010)
Ubiquitin (Housekeeping)	F: GAAGATGGCCGCACTCTTCTGAT R: ATCCTGGATCTTGGCCTTCACGTT	150	GI:57163956/ Frota *et al.* (2011)

Note: F= forward primer; R= reverse primer.

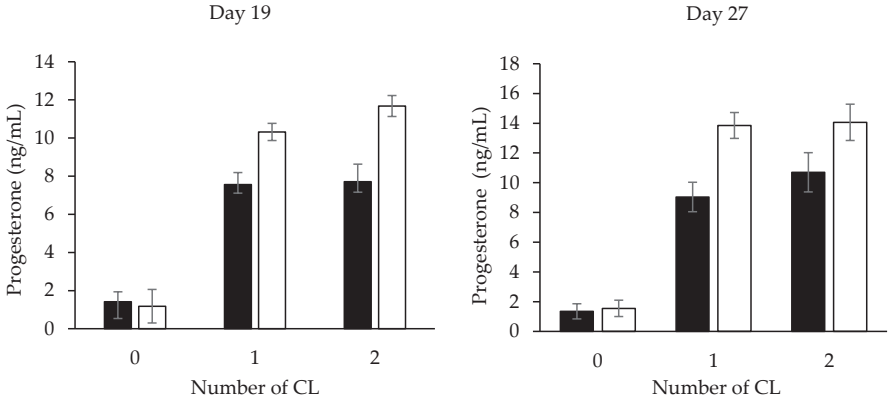

Figure 1. Plasma progesterone concentration in Boer goats based on the number of CLs recorded on Day 19 (left) and Day 27 (right). ■= Control; □= treatment.

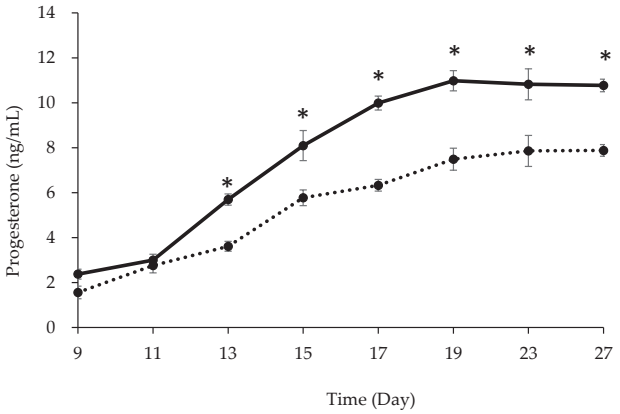

Figure 2. Plasma concentration of progesterone in control (dashed line; n= 9) and supplemented (solid line; n= 8) female Boer goats. Asterisk (*) indicates a significant difference between treatments. Data are the mean ± SEM.

Supplementation did not significantly increase ovulation rate (Control: 1.00 ± 0.24 vs. Supplemented: 1.25 ± 0.25; Table 4). However, supplementation significantly increased the level of expression *PGRMC1* in both follicles and CLs ($p<0.05$; Figure 3). Specifically, *PGRMC1* expression was 2.31-fold greater in follicles and 3.75-fold higher in CLs in the supplemented group compared to the control group. Furthermore, *PGRMC1* expression was positively correlated with circulating progesterone concentrations ($r= 0.65$, $p<0.05$; Figure 4).

Table 4. The number of corpora lutea and ovulation rate (Day 19) in control and supplemented Boer goats

Group	Number of corpora lutea (CL)			n	Ovulation rate ± SEM
	0	1	2		
Control	2	5	2	9	1.00 ± 0.24
Supplemented	1	4	3	8	1.25 ± 0.25

DISCUSSION

In Boer goats, short-term dietary supplementation with concentrate did not increase the ovulation rate or the number or diameter of the corpora lutea but did increase progesterone concentrations and the expression of *PGRMC1* in both follicles and corpora lutea. Both of these effects were independent of changes in live weight or body condition.

The results are contradictory to a previous study based on supplementing goats with protein-rich opuntia, in which the dietary treatment increased the number and diameter of corpora lutea, although the extra luteal tissue did not lead to an increase in circulating progesterone concentrations (Meza-Herrera *et al*., 2019). The different outcomes might be due to differences in the nature of the nutritional supplements, suggesting that the concentrate used influenced metabolic hormones or steroidogenic pathways. Indeed, we observed a significant increase in the expression of *PGRMC1*.

In addition, the presence of exogenous hormones, such as analogs of prostaglandin and progesterone, for oestrus synchronization might affect the ability of supplementation to increase ovulation rate in goats (Meza-Herrera *et al*., 2013; Nogueira *et al*., 2017). The prostaglandin analog, cloprostenol, acts as a regulator of follicle size during folliculogenesis and might be involved in the initiation of the process of follicular rupture for ovulation, thus improving the ovulation rate. In cattle, Martinez *et al*. (2018) examined luteolysis induction and dominant follicle dynamics after treatment with cloprostenol, and concluded that it does not interfere with dominant follicle development but does affect gene expression in granulosa cells, a major factor in the regulation of ovulation. It is thus possible that, in does, combining oestrus synchronization with concentrate supplementation will enhance the ovulation rate (Zabuli *et al*., 2010).

The effects of treatment on circulating P4 concentrations suggest that the concentrate stimulated the growth and function of the CLs. A similar outcome has been reported in other studies of nutritional supplementation in goats (Bomfim *et al*., 2016; Putranto *et al*., 2017; Chaudhari *et al*., 2020). Of particular interest is the study by Chaudhari *et al*. (2020), who showed that dietary supplementation with omega-3 polyunsaturated fatty acids (PUFAs) could influence the expression of genes involved in progesterone biosynthesis in the CL, such as 3βHSD, contributing to higher circulating P4 concentrations in goats. We did not measure the effect

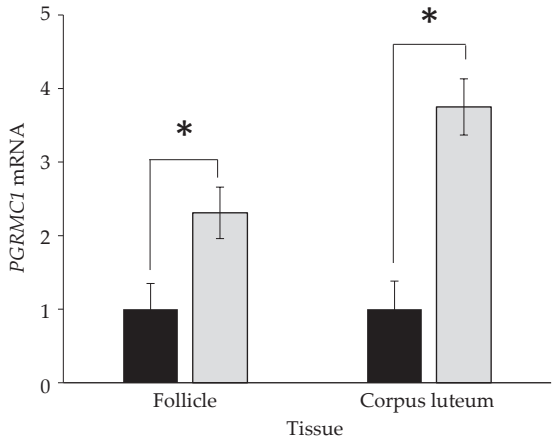

Figure 3. Level of expression of *PGRMC1* in follicular and luteal tissues in Boer goats on Day 27 after CIDR removal. Values are expressed as fold-change ± SD. Asterisk (*) indicates a significant difference ($p<0.05$) between treatments. ■= Control; □= treatment.

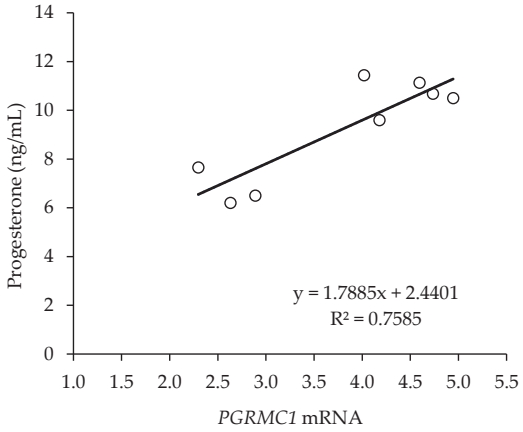

Figure 4. Scatter plots showing the relationships between relative expression of *PGRMC1* gene and plasma concentration of progesterone in Boer goats.

of diet on 3βHSD, but the elevation of *PGRMC1* gene expression in the supplemented group is coherent with stimulation of progesterone biosynthesis because greater P4 concentrations and a positive correlation between P4 concentration and *PGRMC1* expression were observed. The same correlation has also been documented in cattle and humans (Kowalik & Kotwica, 2008; Sueldo *et al*., 2015).

Nutrition is considered to exert effects directly on the ruminant ovary through metabolic factors, such as leptin, insulin, and adipokines (review: Juengel *et al*., 2021). This raises the possibility that luteal function in goats could be stimulated by a concentrate supplement because these factors can act directly on follicles and the CL. Our observations suggest that follicular and luteal *PGRMC1* could play a role in that process, thus affecting progesterone secretion – indeed, progesterone has been shown to control its own synthesis through *PGRMC1* (Rekawiecki *et al*., 2017). Two mechanisms that enhance steroidogenesis by increasing the synthesis of cholesterol might explain the response to supplementation in the present study. First, *PGRMC1* can directly bind two proteins, insulin-induced gene-1 (INSIG1) and sterol regulatory element-binding protein cleavage-activating protein (SCAP), to increase the transcription of sterol regulatory element-binding protein, thus enhancing steroid synthesis through steroidogenic acute regulatory protein, StAR (Yang *et al*., 2002; Manna *et al*., 2015; Stocco & Selvaraj, 2017). Second, *PGRMC1* binds and activates the cytochrome P450 enzyme, P450 protein Cyp51/lanosterol demethylase, catalyzing an essential reaction in the sterol synthesis pathway (Lepesheva & Waterman, 2007).

In follicles, increased *PGRMC1* expression may slow down follicular development by suppressing intracellular signaling pathways, such as p-ERK1/2, p-p38, and p-NF-κB that are involved in cell differentiation and steroidogenesis (Yuan *et al*., 2018), thus inhibiting follicular steroidogenic enzymes (StAR and cholesterol side-chain cleavage enzyme) and limiting oestradiol production. The combined effect could reduce negative feedback on GnRH secretion, thereby allowing increased LH secretion, which would further support CL function and progesterone production.

It is important to note that this study did not directly measure the intracellular pathways or mechanisms described, and while the proposed roles of *PGRMC1* in follicular and luteal function provide a plausible explanation, further investigation is required.

CONCLUSION

This study has shown that short-term supplementation with concentrate can increase the expression of *PGRMC1* in follicular and luteal tissues in the goat. The supplement did not increase ovulation but did increase circulating progesterone concentrations, an outcome that was perhaps mediated by the effects on *PGRMC1* expression. The increases in P4 concentration and *PGRMC1* expression in the supplemented does might also have had anti-mitotic effects in follicles, thus supporting the production of P4. As a consequence, concentrate supplementation has the potential to maintain the growth and development of embryos during the luteal phase and early pregnancy in female goats.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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