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Comparison of follicular dynamics and hormone profiles in Boer goats examined during the breeding and non-breeding seasons in the tropics of Queensland, Australia

D.M. Nogueira [a,b,*] , J. Cavalieri [b], B. Gummow [b,c], A.J. Parker [b]

[a] Embrapa Semiárido, BR 428, Km 142. Caixa Postal 23. CEP 56300-972, Petrolina-PE, Brazil.

[b] College of Public Health, Medical and Veterinary Sciences, James Cook University, Townsville, QLD 4811, Australia.

[c] Faculty of Veterinary Science, University of Pretoria, Pretoria, South Africa.

Abstract. This study aimed to describe ovarian follicular dynamics in Boer goats (n = 14) during the breeding and non-breeding seasons in the tropics of Queensland. Progesterone profiles and follicular dynamics were compared over a 21-day period in the non-breeding season and one oestrous cycle in the breeding season. Between September and October, 100% of goats were in anoestrus while between April and May they were all undergoing ovulatory cycles. The number of follicular waves during a 3-week period of monitoring was greater during the non-breeding compared to the breeding season (4.8 ± 0.1 vs 4.1 ± 0.1, respectively; $P < 0.05$), while the number of codominant follicles (5.6 ± 0.3 vs 6.8 ± 0.3, respectively; $P < 0.05$), growth rate (0.61 ± 0.05 mm/day vs 0.81 ± 0.05 mm/day, respectively; $P < 0.05$) and the diameter of the largest follicle measured within follicular waves (6.7 ± 0.1 mm vs 7.8 ± 01 mm, respectively; $P < 0.05$) were less in the non-breeding compared to the breeding season. During the breeding season the interovulatory interval was 19.7 ± 0.2 days. Total number of small follicles (2 to 3 mm) and the total number of follicles ≥3 mm from Days 2 to 14 of the period of examination were greater ($P < 0.05$) during the non-breeding compared to the breeding season. In the breeding season, 35.7% of cycling goats showed large anovulatory follicles, which persisted and became luteinized. Ovulatory follicles were derived from the fourth follicular wave in 71% of goats. These results have described differences in characteristics of follicular development in the same Boer goats examined during the breeding and non-breeding seasons. In the non-breeding season, the ovaries remained active and follicles continued to grow to reach the equivalent size of preovulatory follicles. Follicular dynamics in the

* Corresponding author. +61 4 8894 3333. Email addresses: daniel.nogueira@embrapa.br , daniel.maianogueira@my.jcu.edu.au

breeding season was characterised by the development of larger follicles and greater follicular growth rates. Short oestrous cycles and follicular cysts may reduce ovulation rate in Boer goats in the breeding season.

Keywords: Anoestrus, goats, oestrous cycle, progesterone, reproduction, seasonality.

1. Introduction

Goats are by nature seasonal breeders. This seasonality of reproductive cyclicity is related to the annual variations in photoperiod (Fatet et al., 2011). The breeding season is stimulated by a reduction in the hours of daylight (negative photoperiod), with the largest percentage of conceptions occurring in autumn and winter. Conception within autumn and winter results in kidding during spring, when feed supply and environmental conditions are usually most favourable (Scaramuzzi et al., 2006; Fatet et al., 2011).

Some authors have claimed that Boer goats are not seasonal breeders (Malan, 2000) and that a complete period of seasonal anoestrus has never been observed in Boer goats (Greyling, 2000). In Townsville (19°19' S), which is located within a tropical region of north QLD, Boer goats fed with an above maintenance diet were recorded to be in anoestrus in November and the timing of the commencement of the breeding season was distributed from December to April; with most goats starting to ovulate in March (Nogueira et al. 2015).

There are a limited number of reports that have studied follicular dynamics in anoestrous goats with most studies reporting on follicular dynamics in does that are undergoing oestrous cycles (Ginther and Kot, 1994; Menchaca and Rubianes, 2002; Medan et al., 2005). Previous studies in cyclic goats indicated that ovarian follicles throughout the oestrous cycle exhibited a wave-like pattern, with two or more follicles attaining 5 mm or more in diameter and growing approximately 1.0 mm per day (Ginther and Kot, 1994; Medan et al., 2003; Simões et al., 2006). In anoestrus Anglo-Nubian and Saanen goats, the ovaries remained active and antral follicles continued to grow in a wave-like pattern with the largest follicles within follicular waves reaching the equivalent size of preovulatory follicles (Cruz et al., 2005). No information, however, appears to be available regarding follicular dynamics in Boer goats maintained in the tropics of Australia, and there are no reports that have compared follicular dynamics in the same goats when they are seasonally anoestrous and when they are undergoing oestrous cycles.

Understanding the patterns in follicular dynamics in does between the non-breeding and breeding season may help to illuminate physiological causes of differences in fertility and prolificacy when goats are bred at different times of the year. The aim of this study was to describe the ovarian follicular dynamics in Boer goats during non-breeding season and the following breeding season in the tropics of Queensland.

2. Material and Methods

2.1 Location, animals and evaluation period

The experiment was carried out at James Cook University, Townsville (19˚19'30" S; 146˚45'44" E) between August 2011 and May 2012. A total of 14 nulliparous and non-pregnant Boer does were used in this study. Animals were evaluated during two consecutive periods: the non-breeding season (September to October; mean dark:light hours, 11.5:12.5) and the following breeding season (April to May; mean dark:light hours, 13:11; Timeanddate, 2014). In the non-breeding season, the mean (± SEM) age and bodyweight of the does were 1.5 ± 0.4 years and 41.3 ± 0.7 kg, respectively. In the breeding season, the mean (± SEM) age and bodyweight of the does were 2.1 ± 0.4 years and 45.7 ± 0.7 kg, respectively. During each period, animals were monitored for four weeks with the aim of documenting and comparing concentrations of progesterone and follicular dynamics over a 21-day period in the non-breeding season and one oestrous cycle during the breeding season. The same 14 replicates were used in the non-breeding and breeding seasons. All experimental procedures for this study were approved by the Animal Ethics Committee of James Cook University (approval number: A1695).

2.2 Animal management

All female goats were maintained on a ryegrass (*Lolium multiflorum*) dominated pasture in the absence of male goats and supplemented daily with lucerne hay in order to provide nutritional requirements above maintenance (7.6 MJ ME/day) for a goat weighing 40 kg (NRC, 2007). Does were observed twice daily for behavioural signs of oestrus with one mature buck for 30 min. Does which allowed the buck to mount were classified as being in oestrus. Intromission by the buck during mounting was prevented by manual withdrawal of the buck from the doe before mating occurred. The bodyweights of all animals were monitored once every two weeks from August 2011 to May 2012 (Fig. 3).

2.3 Blood samples and Progesterone assays

Blood samples were collected once weekly from August 2011 to May 2012 from the jugular vein into evacuated tubes (BD Vacutainer®, Plymouth, UK) containing lithium heparin. During the 21-day periods in which follicular dynamics were being monitored in the non-breeding and breeding season, blood samples were collected once every second day. After collection, blood samples were centrifuged at 2500 g for 15 minutes, then plasma was isolated and frozen (-20^{o}C) until the time of assay.

Concentrations of progesterone in plasma were determined by Radioimmunoassay (RIA) using anti-progesterone antibody-coated tubes (RIA Progesterone IM1188, Beckman Coulter Australia Pty Ltd, Yeerongpilly, QLD). The sensitivity of the assay was 0.05 ng/mL. The intra-

assay coefficients of variation for low (0.80 ng/mL) and high (4.55 ng/mL) quality controls were 4.1% and 3.5%, respectively. The corresponding inter-assay coefficients of variation were 13.8% and 9.7%, respectively. Concentrations of progesterone above 1 ng/mL was used as an indication of ovulation (Thimonier, 2000).

2.4 Synchronization of oestrus and ultrasonography

During the breeding season Boer goats had their oestrous cycles synchronized with two injections of cloprostenol (125 µg IM; EstroPlan®, Parnell Australia Pty Ltd, Alexandria, NSW), given seven days apart. During the breeding season goats were monitored with transrectal ultrasound evaluations using a 6.6 MHz transducer (MyLab^{TM} FiveVET, Medical Plus Australia Pty Ltd, Tullamarine, Vic) once daily after administration of the last dose of cloprostenol to detect ovulation with examinations continuing until the next ovulation was recorded. During the non-breeding season data were recorded over a 21-day period following the retrospective identification of follicular wave emergence.

Video recordings of each ultrasound examination were made. All follicles $\geq$2 mm in diameter and corpora lutea were measured using electronic calipers and ovarian maps were drawn. A follicular wave was defined as one or more antral follicles growing from 3 to $\geq$5 mm in diameter before subsequently regressing and being no longer detectable. The day of emergence of follicles was identified as the day on which the dominant follicle within a given follicular wave was retrospectively first observed to be ≥3 mm in diameter. The end of a follicular wave was recorded when dominant follicle(s) associated with a follicular wave could no longer be identified. Individual follicles emerging within a 48-hour period of the day of emergence of the dominant follicle were regarded as belonging to the same follicular wave. The duration of a follicular wave was defined as the interval between the day of emergence and the day this follicular wave could no longer be identified. The interwave interval was recorded as the number of days between the start of two sequential follicular waves. Follicular growth rate (mm/day) was the time taken by a follicle to grow from the first time it was observed (≥2 mm in diameter) to its maximum diameter. The day of maximum follicular diameter was the first day in each wave when dominant follicles reached a maximum diameter ≥5 mm. Follicles were classified as codominant when two or more follicles $\geq$5 mm were present within the same follicular wave. When codominant follicles were observed only data related to the largest follicle was used for the purposes of analyses related to the assessment of follicular waves. The day of ovulation was defined by the sudden loss of a follicle $\geq$5 mm in diameter followed by the development of a corpus luteum within same ovary. During the breeding season the day of ovulation was defined as Day 0. During the non-breeding season, Day 0 was the day of emergence of a new follicular wave. The interoestrus and interovulatory intervals were

defined as the interval between the detection of two successive periods of oestrus and ovulations, respectively. The total number of corpora lutea observed in the ovaries of each doe was recorded as the ovulation rate for each doe. During the present study, all ultrasound examinations were performed by the same operator.

2.5 Statistical analyses

Statistical analyses were conducted using the statistical software package IBM SPSS Statistics for Windows, Version 22.0 (IBM Corp. Released 2013, Armonk, NY). Analysis of variance (ANOVA) was used to compare the effects of season on the number of follicular waves, number of codominant follicles, the maximum diameter of the largest follicle in each wave, duration of a wave, the interwave interval, growth rate of follicles, number of ovulations, and number of small (2 to 3 mm), medium (>3 and <5 mm) and large follicles (≥5 mm). Interactions included in the ANOVA model were between the effects of the non-breeding and breeding season and between each season and the order in which follicular waves (1^{st}, 2^{nd}, 3^{rd} or 4^{th} waves) were recorded during the period of observation. Differences in means between the non-breeding and breeding seasons were compared using a paired t-test. Repeated measures analysis of variance was used to compare the mean total number of small, medium and large follicles, and plasma concentrations of progesterone from Days 1 to 21 between goats in the breeding and non-breeding season. If the Mauchly's test indicated violation of the assumption of sphericity, probability values were obtained after degrees of freedom were adjusted using Greenhouse-Geisser statistic. The data expressed as percentages were compared by Chi-square test. Results are presented as mean ± SEM and differences were considered significant when $P < 0.05$.

3. Results

3.1 Timing of the breeding and non-breeding season

Weekly assessment of concentrations of progesterone indicated that during August 43% (6/14) of does were in anoestrus, and between September and October 100% of does were in anoestrus. A small percentage of goats (7.1%; 1/14) commenced cycling in November and by April 100% of does were cycling (Fig. 1). In the non-breeding season (September and October), oestrous behaviour was not observed and ovulation was not detected. Concentrations of progesterone were always less than 0.65 ng/mL when does were sampled in the non-breeding season (Fig. 2).

3.2 Bodyweight

The bodyweights of all animals increased ($P < 0.05$) throughout the experimental period (Fig. 3).

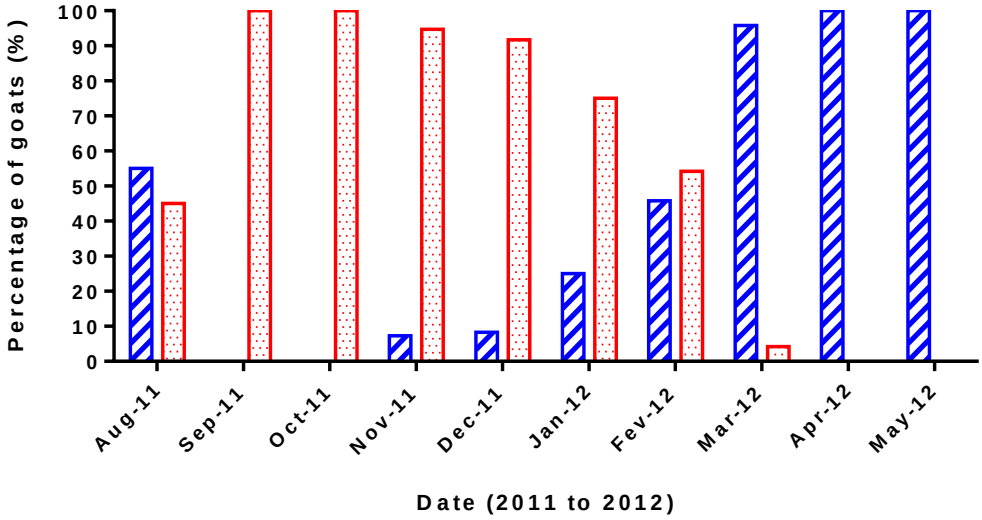

Fig. 1: Percentage of Boer goats ovulating (▨) and in anoestrus (▩) during the experimental period.

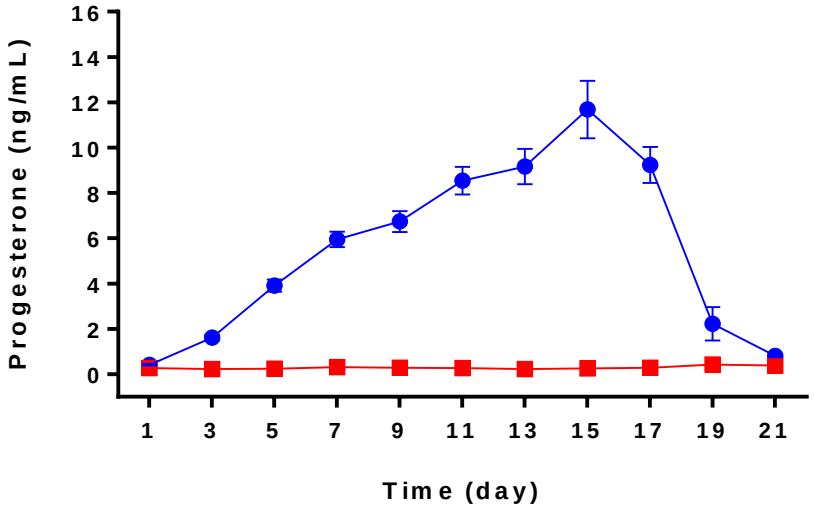

Fig. 2. Concentrations of progesterone in Boer goats during one period of 21 days in the breeding (●) and non-breeding (■) seasons.

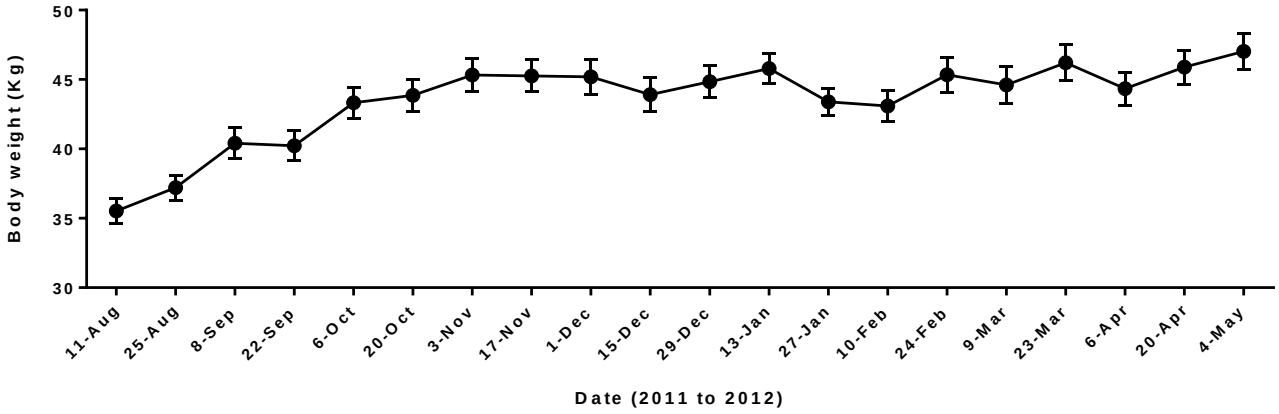

Fig. 3: Variation of bodyweight of Boer goats during the experimental period.

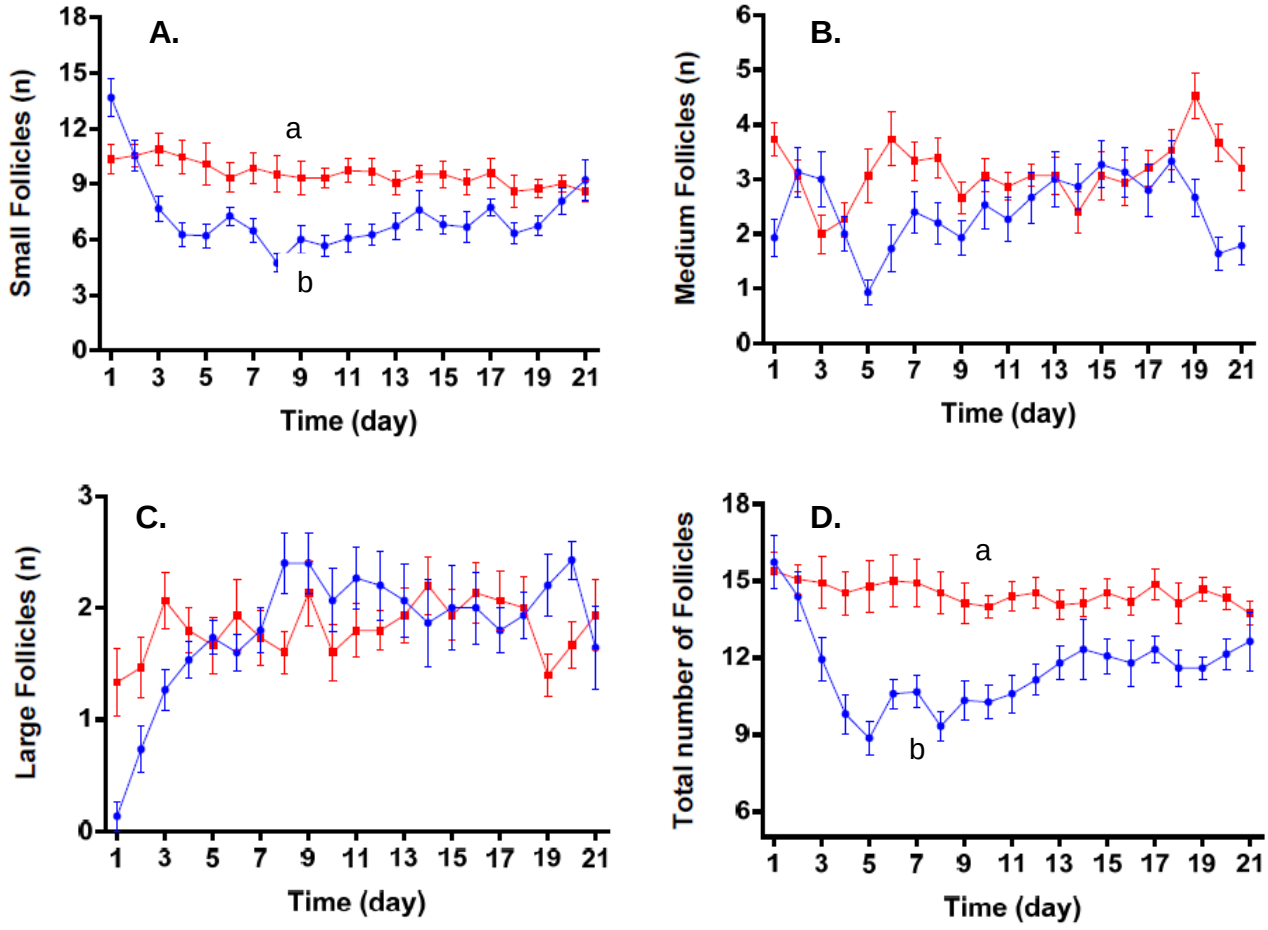

Fig 4. Number of (**A**) small (2 to 3 mm), (**B**) medium (>3 and <5 mm), (**C**) large (≥5mm), and (**D**) total number of follicles ≥ 3 mm during 21 days of ultrasound evaluations of Boer goats during the non-breeding (■) and breeding seasons (●). (ab: within seasons differ; P<0.05).

3.3 Follicular dynamics

The mean number of follicular waves during the 21-day recording period was greater ($P < 0.05$) during the non-breeding compared to the breeding season, while the mean number of codominant follicles was greater ($P < 0.05$) in the breeding season (Table 1). In the non-breeding season, 64% (9/14) of goats had five follicular waves, while in the breeding season 71% (10/14) of goats had four waves (Table 1).

Significant differences in characteristics of follicular development were found between the non-breeding and breeding seasons, and significant interactions were observed between the diameter of the largest follicle and the order of follicular waves, and the duration of waves and order of follicular waves during the breeding season (Table 2). The mean diameter of the largest follicle that was recorded during the period of observation in each season was greatest during the breeding season. The diameter of largest follicles recorded in Waves 2 and 3 were similar ($P > 0.05$) between the non-breeding and breeding season. However, the diameter of the largest follicle in Waves 1 and 4 during the breeding season was greater ($P < 0.05$) compared to the largest follicle in comparable waves during the non-breeding season (Table 2).

In the breeding season, the duration of a follicular wave was greatest for Wave 1 and shortest for Wave 4 (Table 2; $P < 0.05$). The mean duration of follicular waves was similar between the non-breeding and breeding season. However, duration of Wave 4 in the breeding season was shorter ($P < 0.05$) than that in the non-breeding season (Table 2). Overall, the growth rates of follicular waves were greater ($P < 0.05$) in the breeding season compared to the non-breeding season. The mean interwave interval between the non-breeding and breeding season were similar (Table 2).

The number of small, medium and large follicles and the total number of follicles during 21 days of ultrasound evaluations are shown in Figure 4. The mean number of medium and large follicles during the examination periods did not differ ($P > 0.05$) between the breeding and non-breeding seasons and no significant interactions between day and season were detected for these variables (Fig. 4b and Fig. 4c). Significant interactions between day and season were detected for the number of small follicles (Fig. 4a) and the total number of follicles (Fig. 4d). On Day 1, the number of small follicles was greater ($P < 0.05$) in the breeding season compared to the non-breeding season; however, between Days 2 and 14 the number of small follicles and the total number of follicles were greater ($P < 0.05$) during the non-breeding season.

Characteristics of the oestrous cycle in the breeding season are listed in Table 3. The number of ovulations recorded following the synchronized oestrus was similar ($P > 0.05$) to the number that occurred following a non-synchronized oestrus. The interovulatory interval observed by ultrasound was one day shorter ($P > 0.05$) than the interoestrus interval (Table 3). After the synchronized

Table 1: The number of follicular waves found in Boer goats during a 21-day period of observation conducted in the breeding and non-breeding season.

	Non-breeding season (n = 14)	Breeding Season (n = 14)
Follicular waves (n)	4.8 ± 0.1^{a}	4.1 ± 0.1^{b}
Codominant follicles (n)	5.6 ± 0.3^{a}	6.8 ± 0.3^{b}
Goats with 3 waves, % (n)	0.0^{C}	$7.1\ (1/14)^{C}$
Goats with 4 waves, % (n)	$28.6\ (4/14)^{aC}$	$71.4\ (10/14)^{bD}$
Goats with 5 waves, % (n)	$64.3\ (9/14)^{aD}$	$21.4\ (3/14)^{bC}$
Goats with 6 waves, % (n)	$7.1\ (1/14)^{C}$	0.0^{C}

[ab] Values between seasons differ ($P < 0.05$).
[CD] Values within the same season differ ($P < 0.05$).

Table 2: Mean ± SEM characteristics of follicular development during a 21-day period of observation during the non-breeding and breeding season in Boer goats.

Parameters	Non-breeding season (n = 14)	Breeding Season (n = 14)
Largest follicle of wave 1 (mm)	6.2 ± 0.2^{a}	7.2 ± 0.2^{bC}
Largest follicle of wave 2 (mm)	6.3 ± 0.1	6.5 ± 0.1^{D}
Largest follicle of wave 3 (mm)	6.3 ± 0.2	6.6 ± 0.2^{DE}
Largest follicle of wave 4 (mm)	6.2 ± 0.2^{a}	7.1 ± 0.2^{bCE}
Duration of wave 1 (days)	8.5 ± 0.4^{a}	9.6 ± 0.4^{bC}
Duration of wave 2 (days)	8.3 ± 0.3	8.3 ± 0.3^{CD}
Duration of wave 3 (days)	8.5 ± 0.4	7.4 ± 0.4^{D}
Duration of wave 4 (days)	8.4 ± 0.4^{a}	5.9 ± 0.4^{bE}
Largest follicle of all (mm)	6.7 ± 0.1^{a}	7.8 ± 0.1^{b}
Duration of all waves (days)	8.4 ± 0.2	7.8 ± 0.2
Interwave interval (days)	4.4 ± 0.2	4.2 ± 0.4
Growth rate (mm/days)	0.61 ± 0.05^{a}	0.81 ± 0.05^{b}

[ab] Values between seasons differ ($P < 0.05$).
[CDE] For similar parameters, values within the same season differ ($P < 0.05$).

oestrus with cloprostenol, 14.3% (2/14) of does had short cycles. In these animals, a second ovulation was observed six days after the first ovulation.

The ovulatory follicle was derived from the fourth follicular wave in 71.4% (10/14) of goats. Boer goats had a naturally high incidence of multiple ovulation, with 92.8% (13/14) of goats having double ovulations and one goat (7.1%; 1/14) having a triple ovulation. In 61.5% (8/13) of does with multiple ovulations, ovulatory follicles were originated from the same follicular wave and the same ovary, but 38.5% (5/13) of multiple ovulations originated from the same follicular wave but from different ovaries. Two ovulations from different follicular waves were observed in 7.1% (1/14) of oestrous cycles. In the one goat in which this was observed, a second ovulatory wave emerged four days after the first ovulatory wave.

In 35.7% (5/14) of does that had ovulated at the start of the period of monitoring during the breeding season, a follicle within the same cohort as the ovulatory follicles did not ovulate but, instead, persisted and became luteinized. The average maximum diameter of these large anovulatory follicles was 11.2 ± 0.4 mm which was greater than the mean diameter of ovulatory follicles (7.4 ± 0.3 mm, Table 3; P = 0.001). The size of these follicles, therefore, resembled follicular cysts. These goats ovulated after the next natural oestrus and had an interovulatory interval of 19.7 ± 0.2 days. The ovulation rate of goats having a follicular cyst compared to those that did not have a follicular cyst was 1.4 ± 0.3 versus 2.0 ± 0.2, respectively (P = 0.128).

4. Discussion

This study compared the follicular dynamics and progesterone profiles of Boer goats during the breeding and non-breeding season in a tropical region in northern Queensland. To the authors' knowledge this is the first report to describe follicular dynamics of the same Boer goats examined during both the non-breeding and breeding seasons. This study confirmed the occurrence of a natural non-breeding season in Boer goats during the summer period (September to October) at latitude of 19°19'30" South.

Previous studies that have examined follicular dynamics during the oestrous cycle of goats suggest that there are between two and six waves of follicular development during an oestrous cycle with an average of four waves per cycle (Ginther and Kot, 1994; de Castro et al., 1999; Menchaca and Rubianes, 2002; Medan et al., 2005; Simões et al., 2006). Our findings are in agreement with these studies with the recording of a mean of 4.5 follicular waves during the oestrous cycle. The number of follicular waves recorded during a 3-week recording period was greater in the non-breeding season compared to the breeding season. However, the number of codominant follicles,

Table 3. Overall characteristics of oestrus cycle of Boer goats during the breeding season in the tropics of QLD, Australia.

Variables	mean ± SEM
Ovulations after a synchronized oestrus with cloprostenol (n)	1.8 ± 0.2
Ovulations after a natural oestrus (n)	2.1 ± 0.1
Interovulatory interval (days)	19.7 ± 0.2
Interoestrus interval (days)	20.7 ± 0.2
Max diameter of preovulatory follicle (mm)	7.4 ± 0.3
Emergence to ovulation of the ovulatory follicle (days)	5.3 ± 0.4
Growth rate of ovulatory wave (mm/day)	0.9 ± 0.1
Mean max diameter of CL (mm)	12.1 ± 0.2
Lifespan of the CL observed by ultrasound (days)	17.8 ± 0.3
Mean max concentration of P4 (ng/mL)	13.3 ± 1.7
Day of max concentration of P4	15 ± 0.3
Day of lowest concentration of P4	1.0
Mean luteal phase length (days)[a]	16 ± 0.4
Mean follicular phase length (days)[b]	5 ± 0.3

[a] When concentrations of progesterone in plasma were $\geq$1 ng/mL.
[b] When concentrations of progesterone in plasma were <1 ng/mL.

the maximum diameter of the largest follicle within a follicular wave and main growth rate were greater in the breeding season compared to the non-breeding season.

The presence of follicular waves with codominant follicles has been observed in does both in this study and in other studies (Rubianes and Menchaca, 2003; Gonzalez-Bulnes et al., 2005), but in this study we observed that, in the same animals, more codominant follicles were detected in the breeding compared to the non-breeding season. The greater number of codominant follicles during the breeding season can be explained by greater number of follicles which are recruited and selected, which was evidenced on Day 1 of ultrasound evaluations (Fig. 4a). Follicular recruitment and selection is coordinated by endocrine and paracrine regulation involving changes in the secretion of gonadotrophins and numerous growth factors (Hunter et al., 2004). The number of codominant follicles and the number of ovulatory follicles can be increased by decreasing the sensitivity of the hypothalamo-pituitary-ovarian axis to the negative effect of oestradiol to maintain the concentration of FSH above the threshold level for longer, thus allowing more time for follicles to pass through the so called, "widened gate" (Baird and Campbell, 1998; Hunter et al., 2004; Scaramuzzi et al., 2011).

In the breeding season, the diameter of the largest follicle within waves and the duration of a wave differed between follicular waves. It has previously been reported in goats that the largest follicle of the first and the fourth waves usually attain greater diameters than the largest follicles of second and third waves which is in agreement with our findings (Ginther and Kot, 1994; Simões et al., 2006). In the present study, the shorter duration of the fourth follicular wave compared to the first, second and third follicular waves was probably due to the fourth wave being the ovulatory wave in 71% of goats. Increasing concentrations of progesterone during the first follicular wave and persistence of elevated concentrations of progesterone during the second and third follicular waves prevents a preovulatory LH surge (de Castro et al., 1999; Menchaca and Rubianes, 2002), resulting in a period of persistence of dominant follicles before atresia ensues. The onset of luteolysis and an LH surge coincident with the development of the fourth follicular wave in the majority of goats would contribute to a shorter duration of the fourth follicular wave compared to earlier waves (Ginther and Kot, 1994; de Castro et al., 1999). In contrast, during the non-breeding season, circulating concentrations of progesterone were less than 0.65 ng/mL and were similar throughout the growth of each follicular wave (Fig. 2). This would mean that the gonadotrophic stimulation of follicular development would have been similar throughout the period of monitoring contributing to similar wave dynamics between follicular waves. Furthermore, longer day length in the non-breeding season is known to reduce the secretion of melatonin and to increase the negative feedback of oestradiol, which in turn inhibits the secretion of GnRH and results in a reduction in pulsatile LH secretion (Fatet et al., 2011). A reduction in the frequency of release of LH has been demonstrated

in anoestrous sheep (Bartlewski et al., 2000) and this would contribute to the lower follicular growth rates and the smaller mean maximum diameters of follicles within follicular waves that were observed in the non-breeding compared to the breeding season in this study. Thus, differences in gonadotrophin secretion (Bartlewski et al., 1999; Bartlewski et al., 2000) would explain why differences were observed in this study in follicle dynamics between waves within the breeding season and differences in follicle dynamics between the breeding and non-breeding seasons.

The mean diameters of the largest follicle that were obtained in the breeding and non-breeding seasons in this study were similar to those reported previously. Cruz et al. (2005) reported that the mean maximum diameter of the largest follicle during the non-breeding season was 6.5 mm in Anglo-Nubian goats and 6.8 mm in Saanen goats. Medan et al. (2005) reported that during the breeding season that the diameter of the largest follicles in Shiba goats was 6.7 mm in anovulatory waves and 8.0 mm in ovulatory waves, which was similar to what we observed in Boer goats in the current study.

In the present study, we found that mean growth rates were significantly less in the non-breeding (0.6 mm/day) compared to the breeding season (0.8 mm/day) and somewhat less than those previously reported. In the breeding season, follicular growth rates between the day of emergence and the day of maximum diameter have been reported to be approximately 1.0 mm/day (Ginther and Kot, 1994; Medan et al., 2003; Simões et al., 2006). The lesser growth rates reported in this study in both seasons compared to the results of others could be attributed to differences in breeds and age (Ginther and Kot, 1994; de Castro et al., 1999; Driancourt, 2001) and greater exposure to sexually active bucks in some studies (Delgadillo et al., 2011). In anoestrus goats raised in subtropical latitude, follicles increased their growth rate after the introduction of bucks from 1.1 mm/day to 1.5 mm/day (Delgadillo et al., 2011). Furthermore, in the breeding season increasing secretion of LH would have likely maintained faster follicular growth rates compared to during the non-breeding season (Ginther and Kot, 1994; Evans, 2003). Increases in LH pulses following luteolysis would also have contributed to the shorter mean duration of the last follicular wave during the observation period and increased follicular growth rates during the breeding season compared to the non-breeding season.

The reasons why there was a significantly greater number of small and total number of follicles in the non-breeding season when compared to the breeding season is unclear from the results of this study (Fig. 4). In Western White-faced ewes, Bartlewski et al. (1998) also reported a greater number of small and medium antral follicles as anoestrus advances, but the causes remained unknown. In our study, the presence of larger follicles in the first and fourth waves during the breeding season could have obscured the presence of smaller follicles, thereby reducing the total number of follicles that were visible in the breeding season. Another possible explanation for these

results is that during the breeding season the presence of a greater number of codominant follicles resulted in a decrease in the number of small follicles being counted, as more gonadotrophin-responsive follicles within the cohort tended to progress to larger diameters. On the other hand, in the non-breeding season more follicles are arrested at the gonadotrophin independent phase of development and a lower number of follicles are able to progress further in their development because of the lower concentrations of FSH and LH (Driancourt, 2001), which could be one cause of the greater number of smaller follicles being observed during the non-breeding season.

The duration of the oestrous cycle observed in Boer goats (20.7 ± 0.2 days) and the number of ovulations (2.1 ± 0.1) after natural oestrus were similar to those reported in Boer goats and other breeds (Ginther and Kot, 1994; Greyling, 2000; Medan et al., 2005; Simões et al., 2006). In 7.1% (1/14) of goats that double ovulated, the ovulatory follicles emerged as part of two different follicular waves that emerged at different times. Similar results have been previously reported by Ginther and Kot (1994), in 10% (2/20) of the interovulatory intervals in Saanen goats, and by Gonzalez-Bulnes et al. (2005) in 20% (3/15) Murciano-Granadina goats. These results confirm that the phenomenon observed is uncommon being evident in 12.2% (6/49) of goats when the results of these three studies are combined. Ovulation of dominant follicles from earlier follicular waves can be explained by older dominant follicles losing functional dominance and thus enabling a new ovulatory follicle to emerge, but still appear to retain the ability to ovulate in the presence of a preovulatory LH surge (Gonzalez-Bulnes et al., 2005).

The present study showed that the mean maximum concentration of progesterone (13 ng/mL) was attained around Day 15 of the oestrous cycle (Fig. 2), which agrees with de Castro et al. (1999) who reported that progesterone profiles in all Saanen goats started to decline on Day 15 and attained basal level on Day 19 of the interovulatory interval. The lifespan of corpora lutea observed by ultrasound (18 days) was longer than the duration of the luteal phase (16 days). These results are in agreement with Castro el al. (1999) who reported the corpora lutea remained detectable by ultrasound after a significant decrease in progesterone concentration.

This study has highlighted the occurrence of factors that could reduce reproductive performance in Boer does in a tropical environment. These include the occurrence of short oestrous cycles, cystic follicles and differences in the number of codominant follicles between the breeding and non-breeding seasons. During the breeding season, 14.3% of does experienced short cycles and 35.7% of does developed ovarian follicles that resemble follicular cyst. These results might be compounded by the administration of cloprostenol during the breeding season, as cloprostenol was not administered in the non-breeding season. Thus, in this study, it is not possible determine if these short cycles and follicular cysts were associated in goats during transition from the non-breeding to the breeding season (de Castro et al., 1999) or induced with the administration of cloprostenol. In

other species, such as cows, short oestrous cycles and premature ovulations can be induced with cloprostenol and gonadotropin-releasing hormone (Taponen et al., 2002). Perhaps, following administration of cloprostenol in some does, the rapid onset of pro-oestrus led to the induction of a preovulatory LH surge, but the emerging dominant follicles differed slightly in their degree of maturity with one being mature enough to ovulate and the other not having a sufficient number of LH receptors to ovulate (Garverick et al., 1992). The development of follicular cysts could potentially reduce ovulation rate, although further work with a greater number of animals is needed to determine if ovulation rates are significantly reduced in does with cystic follicles.

5. Conclusions

These results have identified a period of anoestrus in Boer goats maintained at latitude 19º19'S, that extended in over 90% of goats from September to December, and have described differences in follicular dynamics in the same Boer goats examined during the breeding and non-breeding seasons. The pattern of follicular dynamics over 21-day period was most frequently characterized by four follicular waves in the breeding season and five waves in the non-breeding season, but the number of codominant follicles within waves was greater in the breeding season. In the non-breeding season the ovaries remained active and follicles continued to grow to reach the equivalent size of preovulatory follicles. Follicular dynamics in the breeding season compared to the non-breeding season was characterised by the development of larger follicles and greater follicular growth rates. Short oestrous cycles and follicular cysts may also potentially reduce ovulation rate in Boer goats in the breeding season.

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