Pre-ovulatory follicular characteristics and ovulation rates in different breed crosses, carriers or non-carriers of the Booroola or Cambridge fecundity gene

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Abstract

Terminal follicular dynamics and ovulation rates (OR) were compared in different local breeds after introducing fecundity genes of different origin. Crossbred ewes which were carriers (F +) or non-carriers (++) of Booroola (BFec) or Cambridge genes (CFec) were included: Cambridge × Cambridge (CC), Cambridge × Suffolk (CS), Cambridge × Texel (CT), Booroola × Texel (BT) and Booroola × German Mutton Merino (BGM). The numbers of small (diameter 2–3.5 mm), medium (diameter >3.5–5.0 mm) and large (diameter >5.0 mm) growing follicles, the maximum diameter before ovulation and the regression and artemia rates of ovarian follicles ≥ 2 mm in diameter were studied laparoscopically and repeatedly during the last 5 days of an induced oestrous cycle. The ORs were determined one cycle before and two cycles after the repeated laparoscopy. BFec and CFec significantly enhanced the OR of all crossbreeds. Carriers of BFec or
C Fec did not have significantly different ORs due to any crossbreeding effect. The same observation was made for non-carriers of both Fec gene types. Whatever the crossbreed, the number of small, medium and large growing follicles were similar between carriers and non-carriers in spite of a higher number of ovulating follicles in carriers of both Fec gene types. The diameter of ovulatory follicles did not differ among crossbreds, or between carriers and non-carriers except in the BT (5.2 ± 0.2 vs. 6.5 ± 0.8 mm, respectively) and CC (6.6 ± 0.2 vs. 5.6 ± 0.3 mm) ewes.

The higher OR in the presence of the Booroola gene was associated with a low atresia rate of large follicles in all crossbreds (BT: 52 ± 8% (f +) vs. 61 ± 7% (+ +); BGM: 51 ± 6% vs. 75 ± 5%). The high OR of the carriers of the C Fec gene seemed to be associated with a lower number of large growing follicles with a lower (P < 0.05) atresia rate as compared with Booroola crossbreds.

In conclusion, follicular features were similar between purebred Cambridge and its crossbred CS and CT. In ewes carrying the B Fec or C Fec gene, the reduction in follicular atresia seemed to be one of the main follicular features implicated in the higher OR.

Keywords: Sheep, Ovary; Fecundity; Genetics; Follicles; Ovulation rate

1. Introduction

The mechanisms by which the ovulation rate (OR) is controlled may differ amongst breeds of sheep (Driancourt et al., 1986; Bindon et al., 1996) and be related to a number of follicular parameters (Driancourt et al., 1986).

It has been shown that in the Booroola Merino, differences in follicle development morphology are involved with differences in OR between carriers and non-carriers. Indeed, the follicle size at the time of ovulation, together with the number of granulosa cells in pre-ovulatory follicles, and the rate of follicle atresia are markedly reduced in the prolific Booroola Merino (Driancourt et al., 1985; McNatty et al., 1987, 1991). It was also reported that Booroola × Romanov carrier ewes had higher numbers of recruitable follicles, smaller follicles size at the time of recruitment and an extended time for recruitment compared to the non-carriers (Driancourt et al., 1986).

Such data are not yet available for the prolific Cambridge breed. This breed is an artificial composite breed produced from various prolific ewes of nine different breeds, with an approximate contribution of 20–25% from the Finnsheep (Owen, 1996). It is now well established that prolificacy in the Cambridge breed is caused by major genes (Fahmy and Davis, 1996).

Even if the heritability of OR is markedly high in prolific sheep (Hanrahan, 1991; Hanrahan and Quirke, 1985), it is not known whether introducing the Booroola or Cambridge fecundity gene in local breeds with low prolificacy to produce heterozygous crossbreds, may lead to similar follicular dynamics as in purebred prolific breeds.

The objective of our study was to compare the terminal follicular growth in purebred Cambridge ewes carriers or non-carriers of the fecundity gene; and to determine the effects of introducing the Booroola or Cambridge fecundity gene into different local
meat breeds; namely, the Texel, Suffolk and German Merino. The comparison focused on the following:

- the effects of the presence of the gene (F + vs. + +);
- the effects of genes of different origin (\( ^{6} \) Fec vs. \( ^{6} \) Fec); and
- the effects of crossing a gene in different local breeds (BT vs. BGM, Cambridge \( \times \) Cambridge (CC) vs. CT vs. CS).

A unique feature of this study is that the Booroola and Cambridge crossings were observed simultaneously in similar experimental conditions.

2. Materials and methods

2.1. Animals

The experiment was performed during the breeding season (September–October) at the Ovine Research Centre, Faulx-les-Tombes (50°25’ North and 5°22’ East), Belgium. All ewes were multiparous. Ten purebred Cambridge ewes (CC) and different cross-breeds, 11 Cambridge \( \times \) Texel (CT), 10 Cambridge \( \times \) Suffolk (CS), 12 Booroola \( \times \) Texel (BT) and 10 Booroola \( \times \) German Mutton Merino (BGM) were investigated. For each type of crossbred, five to six adult (aged 2.5–5 years) carriers (F +) and non-carriers (+ +) were used; they were previously selected on the basis of OR and prolificacy.

During the experiment, the animals were housed indoors under natural lighting. They received water and hay ad libitum enriched with 300 g of concentrate composed of cereal, beet pulp and soya.

2.2. Experimental design

Follicular growth during the oestrous cycle of the ewe presents three distinct waves characterized by a period of recruitment of small follicles, their growth and atresia, except in the 3rd wave where one or some follicles escape atresia and ovulate. This study focused on the 3rd wave, beginning on days 12–13 (day of ovulation = Day 0). Daily laparoscopies (Fig. 1) allowed mapping of the follicles at the ovarian surface and the tracing of their individual events, size, growth and atresia or ovulation.

Every ewe was initially synchronized with two intramuscular injections of 100 \( \mu \text{g} \) of prostaglandin \( \text{F}_{2\alpha} \) (PGF\(_{2\alpha}\) 0.4 ml Estrumate\textsuperscript{®}, Coopers) with an interval of 10 days (Days \(-13\) and \(-3\)) to ensure that all the ewes were at the same stage of the oestrous cycle at the beginning of the experiment. The presumed day of ovulation (3 days after the 2nd injection of PGF\(_{2\alpha}\)) was considered as Day 0. The 1st laparoscopic examination was carried out on Day 6 to determine the OR by counting the number of corpora lutea.
From Days 13 (Day -4) to 17 (Day 0 of the following oestrous cycle), laparoscopies were performed daily to monitor the growth and atresia of every ovarian follicle. The position and the diameter of every follicle (diameter $\geq 2.0\ mm$) on the ovarian surface were mapped. Healthy follicles showed a continuing pattern of growth and reached a steady size or ovulated. In the former case, they became atretic and began to regress until disappearing.

In order to determine whether the repetitive laparoscopic examinations affected any of the reproductive processes, the OR was also determined on Day 21. Thereafter, the ewes had a 2nd session of synchrony for a 3rd evaluation of OR.

2.3. Laparoscopy

Each laparoscopic examination was performed using a 5-mm optic fibre and manipulation probe (Richard Wolf endoscope) engraved with a millimetric scale. Local anaesthesia (1 ml of 2% xylocaine) was injected subcutaneously at two places: 3–4 cm anterior the udder and 4–5 cm either side of the midcentral line. The endoscope and the manipulation probe were inserted into the peritoneal cavity at the injection sites. A preliminary study showed that laparoscopy examination of the ovaries allowed the follicles visible on the ovarian surface to be accurately monitored (Noël et al., 1992; 1993).

2.4. Presentation of results

Follicles were ranked into three size classes: small (diameter 2–3.5 mm), medium-sized (diameter $>3.5–5.0\ mm$) and large (diameter $>5.0\ mm$). The following features of follicular growth were calculated: mean number of small, medium-sized and large follicles; maximal size attained by the largest follicles before regression or ovulation; atresia rate; and, OR. The atresia rate was defined as the percentage of shrinking follicles between two size classes.

2.5. Statistical analysis

The data are expressed as means $\pm\ S.E$. They were analyzed using GLM procedures (Statistical Analysis System, 1985). A three-way analysis of variance was used to determine whether OR and follicular parameters differed among crossbreds and between
Fec carriers and non-carriers. In the model, the crossbred type and the fecundity-gene status were considered as fixed-crossed effects, and the ewe was taken as a random effect (Dagnelie, 1975). The Scheffe test was used to compare group means when the main or interaction effects were significant ($P < 0.01$ and $P < 0.05$). Values relating to OR and the rate of follicle atresia were logarithmically transformed before analysis.

3. Results

3.1. Ovulation rate

The results for OR are summarized in Table 1. The OR was higher ($P < 0.05$) in Fec gene carriers ewes than in non-carriers. The carriers of either the Booroola (BGM and BT) or Cambridge (CC, CT and CS) fecundity gene did not have significantly different OR means. The same observations were realized with the non-carriers. Also, the OR data did not differ between purebred CC and its crossbred CS and CT ewes; nor between CT and BT with a fecundity gene of different origin, and between CS and CT with the same fecundity gene.

The OR values did not significantly differ before, at the end of, or 1 month after a 5-day period of laparoscopy, except for the comparison between the 2nd and the 3rd cycles for CS $P < 0.05$.

3.2. Follicular parameters

Data on the follicular parameters are presented in Table 2. Whatever the type of breed, the number of small, medium and large growing follicles did not differ between carriers and non-carriers, despite the higher ($P < 0.05$) number of ovulating follicles in carrier ewes. The number of small growing follicles did not differ among the five experimental breeds. The number of medium-sized follicles was lower ($P < 0.05$) in CC and CT than in CS, BT and BGM crossing irrespective of the fecundity gene status. The number of large growing follicles was lower ($P < 0.05$) in the CT than in other Cambridge ewes and Booroola crossings. Values did not differ between BT and BGM.

The atresia rate for small follicles did not differ between carriers and non-carriers, except for the BT ewes (19 ± 5% $P < 0.05$ vs. 47 ± 5% $P < 0.05$). This rate also did not differ among type of crossbred, except for high ($P < 0.05$) values in the CT and BT ewes. The atresia rate for medium follicles did not differ between carriers and non-carriers and among type of crossbred, with exception of high ($P < 0.05$) values in CS crossbred.

The atresia rates were higher ($P < 0.05$) for large follicles in non-carriers than in carriers, whatever the experimental crossbreed group. Also, they were higher in Booroola crossings than in the Cambridge crossbred (Table 3); they were not significantly different among the three Cambridge groups, nor between the two Booroola crossings.
Table 1
Ovulation rate in the CC, CS, CT, BT and BGM ewes
Values are means ± S.E. a–b (P < 0.05) or b–c (P < 0.01): significantly different means between carriers and non-carriers within each breed or crossbred. Data with no letter indication are not significantly different (P > 0.05).

<table>
<thead>
<tr>
<th>Genotype</th>
<th>CC F+ (n = 5)</th>
<th>+ + (n = 5)</th>
<th>CS F+ (n = 5)</th>
<th>+ + (n = 5)</th>
<th>CT F+ (n = 6)</th>
<th>+ + (n = 6)</th>
<th>BT F+ (n = 6)</th>
<th>+ + (n = 6)</th>
<th>BGM F+ (n = 5)</th>
<th>+ + (n = 5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovulation rate, 1st cycle</td>
<td>3.6 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.0 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.8 ± 0.4</td>
<td>2.2 ± 0.2</td>
<td>3.3 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.0 ± 0.0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.5 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.8 ± 0.6&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.4 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ovulation rate, 2nd cycle</td>
<td>3.2 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.6 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.2 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.0 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.0 ± 0.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.6 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.0 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ovulation rate, 3rd cycle</td>
<td>3.0 ± 0.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.6 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.6 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.3 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.5 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.0 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.8 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.8 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Mean</td>
<td>3.3 ± 0.4</td>
<td>1.9 ± 0.4</td>
<td>3.0 ± 0.3</td>
<td>2.0 ± 0.2</td>
<td>3.2 ± 0.2</td>
<td>1.8 ± 0.2</td>
<td>3.2 ± 0.3</td>
<td>1.8 ± 0.3</td>
<td>3.7 ± 0.4</td>
<td>2.1 ± 0.3</td>
</tr>
</tbody>
</table>
Table 2
Follicular parameters in the CC, CS, CT, BT and BGM ewes
Values are means ± S.E. a–b (P < 0.05) or b–c (P < 0.01); significantly different means between carriers and non-carriers within each breed or crossbred.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>CC</th>
<th>CS</th>
<th>CT</th>
<th>BT</th>
<th>BGM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F+ (n = 5)</td>
<td>+ + (n = 5)</td>
<td>F+ (n = 5)</td>
<td>+ + (n = 5)</td>
<td>F+ (n = 6)</td>
</tr>
<tr>
<td>Number of small follicles</td>
<td>12.6 ± 0.6</td>
<td>12.2 ± 1.0</td>
<td>14.6 ± 1.5</td>
<td>16.0 ± 1.4</td>
<td>12.2 ± 0.9</td>
</tr>
<tr>
<td>Atresia rate (%)</td>
<td>35 ± 5</td>
<td>31 ± 3</td>
<td>27 ± 5</td>
<td>34 ± 7</td>
<td>51 ± 5</td>
</tr>
<tr>
<td>Number of medium follicles</td>
<td>8.2 ± 0.7</td>
<td>8.4 ± 0.8</td>
<td>10.6 ± 1.2</td>
<td>10.4 ± 1.1</td>
<td>5.8 ± 0.3</td>
</tr>
<tr>
<td>Atresia rate (%)</td>
<td>30 ± 9</td>
<td>35 ± 6</td>
<td>48 ± 4</td>
<td>54 ± 1</td>
<td>34 ± 6</td>
</tr>
<tr>
<td>Number of large follicles</td>
<td>5.6 ± 0.5</td>
<td>4.6 ± 0.8</td>
<td>5.4 ± 0.4</td>
<td>4.8 ± 0.6</td>
<td>3.8 ± 0.3</td>
</tr>
<tr>
<td>Atresia rate (%)</td>
<td>42 ± 7a</td>
<td>57 ± 9b</td>
<td>32 ± 5a</td>
<td>51 ± 7b</td>
<td>20 ± 8a</td>
</tr>
<tr>
<td>Diameter of ovulating follicles (mm)</td>
<td>6.6 ± 0.2a</td>
<td>5.6 ± 0.3b</td>
<td>6.2 ± 0.1</td>
<td>6.1 ± 0.5</td>
<td>6.3 ± 0.2</td>
</tr>
</tbody>
</table>

Values represent the percentages of shrinking large follicles as compared with the OR during the 2nd oestrous cycle (Table 1). Data with no letter indication are not significantly different (P > 0.05).
Table 3
Comparison between Booroola and Cambridge crossings

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Cambridge ewes</th>
<th>Booroola ewes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F+ (n = 16)</td>
<td>+ + (n = 15)</td>
</tr>
<tr>
<td>Number of small follicles</td>
<td>13.1 ± 1.0</td>
<td>14.2 ± 1.2</td>
</tr>
<tr>
<td>Atresia rate (%)</td>
<td>37.7 ± 4.9</td>
<td>39.7 ± 4.3</td>
</tr>
<tr>
<td>Number of medium follicles</td>
<td>8.2 ± 0.7</td>
<td>8.5 ± 0.8</td>
</tr>
<tr>
<td>Atresia rate (%)</td>
<td>37.3 ± 6.4</td>
<td>41 ± 4.8</td>
</tr>
<tr>
<td>Number of large follicles</td>
<td>4.9 ± 0.4</td>
<td>4.4 ± 0.6</td>
</tr>
<tr>
<td>Atresia rate (%)</td>
<td>31.3 ± 6.6^a</td>
<td>50.7 ± 9.7^b</td>
</tr>
<tr>
<td>Diameter of ovulating follicles (mm)</td>
<td>6.4 ± 0.2</td>
<td>6.1 ± 0.4</td>
</tr>
<tr>
<td>Ovulation rate</td>
<td>3.2 ± 0.3</td>
<td>1.9 ± 0.3</td>
</tr>
<tr>
<td>Duration of oestrous cycle</td>
<td>16.0 ± 0.6</td>
<td>16.2 ± 0.7</td>
</tr>
</tbody>
</table>

The diameter of ovulatory follicles did not differ among type breeds and between carriers and non-carriers, except in the BT ewes (5.2 ± 0.4 mm F+ vs. 6.5 ± 0.2 mm + +, P < 0.05) and in the CC ewes (6.6 ± 0.4 mm F+ vs. 5.6 ± 0.6 + +, P < 0.05).

4. Discussion

The use of transrectal ultrasonography in sheep is still difficult to perform and to interpret because of problems of anatomical access and with the small size of follicles, as well as the lack of apparent difference between dominant and subordinate follicles (Driancourt, 1994; Driancourt et al., 1991; Souza et al., 1997). For these reasons, we used laparoscopic examinations, even if it is generally thought that this invasive technique may induce a stress, which may interfere with the pituitary secretion and thereby with the reproduction function in some domestic species (Stoebel and Moberg, 1982; Dobson, 1987). In the ewe, however, previous reports have indicated that stress-induced glucocorticoids may have little or no effect on the reproductive mechanisms (Moberg et al., 1981; De Silva et al., 1983; Phillips and Clarke, 1990). The results of the current study showed that the 5-day period of laparoscopy had no effect on the OR of consecutive oestrous cycles.

The overall results concerning OR in the current study confirmed the previous reports that the fecundity gene induced an increased OR (Boulton et al., 1995; Bindon et al., 1996). Data obtained in the two Booroola crossings and those reported by Teyssier et al. (1996: OR = 2.6) indicate that the level of improvement varied according to the base breed in which the Booroola fecundity gene was introduced. Little is reported concerning the comparison between purebred Cambridge CC and its crossbred. In this study,
OR values did not differ between CC carriers ewes and CS and CT ewes. The CC, CS and CT non-carrier ewes had similar values as purebred Suffolk (2.0) and Texel (1.7) of the same population in which the Cambridge gene was introduced (Peeters and Decuypere, personal communication).

The overall follicles $\geq 2$ mm in diameter did not differ between carriers and non-carriers in the BT and BGM crossbred in agreement with a previous finding with heterozygous Booroola Merino $\times$ Romanov ewes $F+$ and $++$ (Driancourt et al., 1986). These findings and another previous report of Driancourt et al. (1985) that Booroola carriers had the same number of antral follicles as the non-prolific Merinos ewes may confirm the hypothesis that follicle numbers do not play a key role in the high OR induced by the Booroola fecundity gene. This hypothesis may be able to be extended to the Cambridge fecundity gene as in the current study, the total number of follicles $\geq 2$ mm did not differ significantly between carriers and non-carriers of purebred CC or CS and CT crossbred. Nevertheless, the finding of Lalhou-Kassi and Mariana (1984) that the number of antral follicles was significantly greater in the D’man prolific breed than in the Timahdite ewes with low prolificacy, indicates that the relationship between the follicle population and the OR may differ among breeds.

Follicles in the small-, medium- and large-sized classes in the present study were respectively considered as recruited, selected and dominant follicles (Noël et al., 1993, 1994a). Their numbers did not differ between carriers and non-carriers, or between the two Booroola crossbreeds. This strengthens the hypothesis that the number of follicles is not related to the increased ovulation. Indeed, it has been reported that Booroola carrier ewes are known to possess a higher number of recruitable follicles than non-carriers and a low intensity of selection (Driancourt et al., 1985, 1986). Data on the main events of follicular dynamics are still scarce in the ewes carrying the $F$ Fec gene. The present study indicated that the number of follicles does not play a key role in the enhancement of OR; in this breed as for the Booroola ewes. Indeed, the numbers of follicles did not differ between carriers and non-carriers in purebred Cambridge CC and its crossbred CS and CT, whatever the follicle-size class.

The comparison of the different types of crossbred indicated that although the numbers of small follicles did not differ, differences were observed among medium and large follicles in relation to rates of atresia. Data on atresia rate of follicles are still inconsistent in literature. The high OR in Booroola ewes is associated with a low atresia rate (Driancourt et al., 1985; McNatty et al., 1987, 1991). In the Romanov and the D’man breeds, the degree of atresia amongst growing follicles was comparable to non-prolific breeds (Lalhou-Kassi and Mariana, 1984). Little is known concerning the correlation between follicular parameters and OR in ewes carrying the Cambridge fecundity gene. The results of this study indicate that the mechanisms by which a high OR may be achieved in the Booroola and Cambridge type breeds did not differ greatly. Indeed, in the carrier ewes the high OR was associated with a low rate of atresia for the large follicles, whatever the origin of the fecundity gene. The only difference was that the Cambridge group ewes had a lower number of large follicles. This was compensated, too, by a lower rate of follicle atresia as compared with the Booroola.

It was previously reported that the ovaries of Booroola carrier ewes were characterized by having significantly smaller follicles at the time of ovulation (Driancourt et al.,
1985; McNatty et al., 1985, 1986). In contrast to this finding, the diameter of ovulatory follicles in the present study did not differ among the different type breeds or between carriers and non-carriers, except in the BT and CC ewes. This may mean that this follicular feature is inconsistent amongst prolific breeds and is as variable as the other aspects of the control of reproduction (Bindon et al., 1996). For all the types of breeds observed in this study, the diameter of ovulatory follicles was smaller (5.20–6.60 mm) as compared with follicular size of some non-prolific purebreds, such as the Texel (7–9 mm, Bister et al., 1988) and Ile-de-France (8.1 ± 0.7 mm, Driancourt et al., 1986). The conventional classification of follicles used for the investigation of follicular development in non-prolific breeds (Noël et al., 1993) may need to be reassessed to determine the timing of emergence for selection and dominance events in prolific breeds.

Previous studies have shown that there are three waves of follicular development in each cycle and that the 3rd emergence of follicles occurred during the luteal phase from around Day 13 (Noël et al., 1993, 1994b). The recruitment of follicles in prolific Booroola ewes takes place over an extended time period between Days 13 and 17 (Driancourt et al., 1985). In the current study, it seemed likely that both ovulating follicles and non-ovulating follicles emerged at about the same time at the beginning of the 3rd wave, triggered by the increase in LH/FSH occurring at this time (McNatty et al., 1985; McNeilly and Fraser, 1987; McNeilly et al., 1986; Ginther et al., 1995). However, more recent studies have indicated that the emergence of this critical wave of follicles during the luteal phase was not always related to fluctuations in the level of LH or FSH (Souza et al., 1997). Perhaps, the developmental differentiation between non-ovulating and ovulating follicles may be related to the increase in intra-ovarian factors from Day −2 (Day 15) due to the emergence of large follicles which thereby prevent the promotion of small follicles.

5. Conclusion

In conclusion, follicular features were similar between purebred Cambridge and its crossbred CS and CT, while the Booroola crossbred seemed to have lost some of the parental purebred Booroola potential. In ewes carrying the \textsuperscript{B}Fec or \textsuperscript{C}Fec gene, the reduction in follicular atresia seemed to be one of the major phenomena contributing to the high OR of both genotypes.

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References


