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REGULAR ARTICLES

Corpora lutea affect in vitro maturation of bovine cumulus-oocyte complexes and embryonic development after fertilization with sex-sorted or conventional semen

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Abstract

Influence of both the presence of a corpus luteum on the ovary and semen sex-sorting on development following in vitro fertilization is not yet conclusive. To determine the effect of these factors, 376 bovine oocytes were processed in vitro according to luteal presence on the ovary (CL+ and CL−) and type of semen used (sexed or conventional). Maturation rate was higher ($P < 0.01$) in CL− (136/138; 98.6%) than in CL+ (217/238; 91.2%). Cleavage rate was lower ($P < 0.01$) in CL+ with sexed semen (60/172; 34.9%) than in CL− with sexed semen (42/71; 59.1%), CL+ with conventional semen (47/66; 71.2%), and CL− with conventional semen (54/67; 85.1%). Compaction was similar ($P = 0.69$) in CL− (49/99; 49.4%) and CL+ (50/107; 46.7%). Blastulation rate was higher ($P < 0.01$) in CL− (26/99, 26.2%) than in CL+ (13/107; 12.1%) group. Expansion rate was higher ($P = 0.01$) in CL− (22/99; 22%) than in CL+ (11/107; 10.2%) group. Compaction rates were similar ($P = 0.78$) in sex-sorted (50/102; 49.0%) or conventional semen (49/104; 47.1%) groups. Blastulation was also similar ($P = 0.91$) with sex-sorted semen (19/102; 18.6%) and conventional semen (20/104; 19.2%). The rate of expanded blastocysts was similar ($P = 0.89$) in sex-sorted (16/102; 15.6%) and conventional (17/104; 16.3%) semen groups. In conclusion, the presence of CL can compromise maturation of the oocytes and their development, as a higher proportion of cleavage-stage embryos can be obtained with non-sexed semen with oocytes from ovaries without a CL.

Keywords Corpus luteum · Sexed semen · In vitro fertilization · Bovine oocytes

Introduction

Embryo production by in vitro fertilization (IVF) of bovine embryos includes oocyte maturation, sperm capacitation followed by fertilization, and embryo culture. Oocyte maturation and sperm capacitation and fertilization are generally accomplished at approximately 24 and 48 h after oocyte collection, respectively, while embryo culture requires approximately 7 days. Oocytes can be obtained either by follicular aspiration in live cows and heifers or by using ovaries from abattoirs (Rehman et al., 2001). The early embryonic development includes cleavage, compaction, blastulation, expansion, hatching, and elongation. These events are essential for the successful establishment of a pregnancy (Peippo et al., 2011), which can be achieved upon transferring an in vitro-produced embryo. The capacity of an egg to generate an embryo largely depends on the developmental competence acquired around or before final maturation inside the follicle (Sirard et al., 2006; Mermillod et al., 2008; Zhang & Smith, 2015). In turn, the follicular environment is influenced by the overall hormonal levels of the animal, as well as the structural and functional status of the ovary (Lucy, 2001; Britt, 2008).

Inconsistent results have been previously reported regarding the effect of the presence of a corpus luteum (CL) on oocyte maturation and its subsequent development after fertilization in many species. Islam et al. (2007) concluded that caprine ovaries without a CL yield an increased number of high-quality oocytes than those with a CL. On the other hand, Aggag et al. (2017) reported that the presence of a CL

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does not affect cleavage, compaction, or blastulation rates in camelids. In contrast, Quezada-Casasola et al. (2018) reported a lower maturation rate of bovine oocytes originated from ovaries with a progesterone-producing CL, which was suggested to exert its negative effect by a paracrine mechanism on the oocyte. On this regard, some authors report contradictory results, stating that progesterone allows the follicle to be exposed for a long period to low-amplitude pulses of LH resulting in better quality oocytes (Pfeifer et al., 2009; Penitente-Filho et al., 2014; Penitente-Filho et al., 2015). It is possible that in addition to that LH pulse effect, the presence of a CL and its progesterone can exert a paracrine effect on the development of the follicle, which could explain the differences observed in quality of oocytes from ovaries with or without a CL (Vassena et al., 2003). In addition, a local effect of the presence of a CL and the corresponding vascularity of the ovary seems to be related to oocyte quality, as the intensity of the angiogenic process reaches its peak in 2 or 3 days after the rupture of the follicle, which increases the blood flow with a proper hormonal environment for the developing follicles (Penitente-Filho et al., 2014). Furthermore, Silva and Knight (2000), Shimada and Terada (2002), and Hajarian et al. (2016) concluded that the presence of progesterone or corpora lutea on the ovary may have a negative effect on the developmental competence of oocytes, since cumulus-oocyte complex (COC) structures coming from ovaries with a CL yielded lower cleavage and blastulation rates after IVF with non-sexed (conventional) semen, when compared with those gametes from ovaries without any CL. However, several reports suggest a potential detrimental impact of sperm sorting on embryonic development after IVF (Palma et al., 2008; Blondin et al., 2009). In relation to that, it is not yet clear the influence of the type of semen, sexed or conventional, on the outcome of embryos generated upon IVF of oocytes originated from ovaries of different status, depending on the occurrence of a CL. Therefore, the objective of the present study was to determine the effect of the presence of corpora lutea on bovine oocyte maturation and their ability to reach cleavage, compaction, blastulation, and expansion stages following IVF either with conventional or sexed semen.

Materials and methods

Except when otherwise stated, all culture media used in the present study were serum-free ready-to-use media from IVF Bioscience (Falmouth, UK) for bovine embryo production and were used according to the manufacturer's instructions.

COCs were harvested from ovaries that showed activity, according to the visual detection of Graafian follicles or an active CL. A CL was considered actively producing progesterone when it measured ≥ 10 mm in diameter, as described by Kastelic et al. (1990). Ovaries were collected from non-pregnant mature Holstein cows slaughtered at a local abattoir in Ciudad Juárez, Mexico, and were placed in one of two containers filled with 0.9% (w/v) saline solution at 35 °C. Ovaries with at least one CL were placed in one container (CL+ group), while ovaries without CL were placed in the other (CL− group). Ovaries were transported to the laboratory under the same controlled temperature within 3 h after collection and upon arrival were washed twice with warm saline solution. Ovaries were kept separated according to the presence or absence of CL at all times.

Immature COCs were collected from all antral follicles of 2–8 mm in diameter using 10-mL syringes and 18- or 20-gauge hypodermic sterile needles. Aspirated follicular fluid from ovaries of CL+ and CL− groups was placed separately into 10-cm previously warmed squared gridded search dishes. A total of 747 COCs were obtained and only those with completely homogeneous or homogeneous with slightly irregularly colored cytoplasm and ≥ 5 layers of compact cumulus cells around the oocyte (scoring categories 1 and 2; Stojkovic et al. 2001) were selected out of the CL+ ($n = 238$) and CL− ($n = 138$) groups. COCs obtained from CL+ and CL− ovaries were handled separately at all times.

After visual selection, CL+ and CL− COCs were washed twice in warm BO-Wash medium and once in BO-IVM maturation medium. Afterwards, COCs were transferred to BO-IVM medium (at a density of 50 COCs per 500 μL pre-equilibrated in a 6% CO_2 atmosphere medium ≥ 2 h) and matured at 38.5 °C in 6% CO_2 with humidified atmospheric air (21% O_2) for 22 h. Maturation of COCs was assessed by determination of the expansion of their cumulus cells, as it was considered when at least few morphological changes in the distribution of the cumulus cells of each COC were observed (Zhang et al. 2010; Caixeta et al. 2013).

After maturation, COCs were washed once in warm IVF medium and then transferred to 400 μL of BO-IVF (pre-equilibrated in a 6% CO_2 humidified atmosphere, ≥ 2 h). In the present study, 250-μL sex-sorted and 500-μL conventional semen straws from previously selected and proven for (IVF) bulls were used. Straws were thawed at 37 °C for 30 s and sperm motility in a sample of each one was evaluated using the AndroVision® software (Minitube, Tiefenbach, Germany) and a computer-assisted sperm analysis (CASA) system. Straws containing sexed semen had a concentration ≥ 1×10^6 cells/mL after thawing and straws containing conventional semen had a concentration of ~ 5×10^6 cells/mL after thawing. Each semen dose was washed twice by centrifugation at 328*g* for 5 min in BO-Semen Prep (previously warmed at 37 °C; 2 and 4 mL for 250-μL and 500-μL straws, respectively). The supernatant was removed both times, leaving approximately 350 and 700 μL of semen suspension for 250- and 500-μL straws, respectively. All COCs were inseminated with the corresponding volume of the final semen solution, in order to get a final sperm concentration of 2×10^6 cells/mL in IVF wells

(containing 400 μL of BO-IVF each). A total of 172 CL+ and 71 CL− COCs were inseminated with sex-sorted semen and a total of 66 CL+ and 67 CL− COCs were inseminated with conventional semen (establishing four experimental groups: CL+ with sex-sorted semen, CL− with sex-sorted semen, CL+ with conventional semen, and CL− with conventional semen). In all four groups, spermatozoa were co-incubated with the corresponding matured COCs in BO-IVF medium (pre-equilibrated in 6% CO_2 atmosphere ≥ 2 h) for 22 h at 38.5 °C in a 6% CO_2 humidified (21% O_2) atmosphere.

Presumptive zygotes of each group were transferred from BO-IVF to BO-Wash medium. Structures were denuded using a vortex mixer (Barnstead International, Dubuque, IA) for approximately 2 min or until they appeared free of their surrounding cumulus cells. Afterwards, the denuded presumptive zygotes were washed in BO-Wash medium, rinsed in BO-IVC culture medium, and cultured in 500 μL of BO-IVC culture medium with a 400-μL BO-Oil overlay in a humidified atmosphere containing 88% N_2, 6% CO_2, and 6% O_2 at 38.5 °C. Cleavage was considered when at least two cells were observed in a single structure during a period of 48 h after the fertilization period; compaction when the cells of the embryo changed from a spherical to a polygonal shape (day 5 after fertilization); blastulation when a clear-colored cavity was observed in the embryo (blastocoel) at day 6 after fertilization; and expansion when an increase in diameter resulting in thinning of the zona pellucida was observed (days 7 to 8 after fertilization; Peippo et al., 2011).

All statistical analyses were carried out using the SAS software (9.0; Statistical Analysis System Institute Inc., Cary, NC). Proportions of matured COCs obtained from CL+ and CL− ovaries (COCs with expanded cumulus cells out of the total COCs used in each group) were compared with chi-square or Fisher's exact tests using the FREQ procedure. Proportions of categorical data of cleavage (number of embryos with an initial cellular division out of the total COCs in each group), compaction (number of compacted morulae out of the total cleaved embryos in each group), blastulation (number of blastocysts out of cleaved embryos in each group), and expansion (number of expanded blastocysts out of the total cleaved embryos in each group) were analyzed initially using the LOGISTIC procedure with a model that included sex-sorted or conventional semen and COCs from CL+ or CL− ovaries as main effects, as well as their interaction. Whenever no interactions were observed, the model was reduced and only the main effects were considered. Values were considered significant when $P < 0.05$.

Results

In the statistical analysis of the proportions of compaction, blastulation, and expansion of embryos, no interaction between the type of semen used (sex-sorted or conventional) and the ovarian status regarding presence or absence of a CL was observed ($P = 0.84$, 0.73, and 0.60 for CL+ with sex-sorted semen, CL− with sex-sorted semen, CL+ with conventional semen, and CL− with conventional semen, respectively). Therefore, the interaction between luteal status of the ovaries and the type of semen used was removed from the original statistical model for these variables. Structures in the CL+ with the sex-sorted semen group showed the lowest proportion of cleavage (60 out of 172; 34.9%), when compared with CL− with sex-sorted semen (42 out of 71; 59.1%), CL+ with conventional semen (47 out of 66; 71.2%), and CL− with conventional semen (54 out of 67; 85.1%) groups, and a significant interactive effect of presence of a CL with sex-sorted semen was observed ($P < 0.01$). Therefore, the original statistical model for this variable was not modified. Proportions of embryo development in all experimental groups after the combined effects of luteal status and type of semen are shown in Table 1. Proportions of COC maturation, as well as compaction, blastulation, and expansion of embryos originated from ovaries with or without a CL as a main effect, are shown in Table 2. A higher proportion ($P < 0.01$) of maturation of oocytes, as determined by the observation of expansion of their cumulus cells, was observed in the CL− group (136 out of 138; 98.6%), when compared with the CL+ group (217 out of 238; 91.2%). Similar compaction rates ($P = 0.69$) were observed in both CL− (49.4%) and CL+ (46.7%) groups (49 out of 99 and 50 out of 107, respectively). Embryos in the CL− group had a higher proportion ($P < 0.01$) of blastulation (26 out of 99; 26.2%) than those in the CL+ group (13 out of 107; 12.1%). Finally, 22 out of 99 blastocysts in the CL− group showed expansion (22.2%), which was higher than the 10.2% observed in the CL+ group (11 out of 107; $P = 0.01$).

Proportions of compaction, blastulation, and expansion of embryos obtained from oocytes fertilized with conventional or sex-sorted semen as a main effect are shown in Table 3. Similar compaction rates ($P = 0.78$) were observed when either sex-sorted (50 out of 102; 49.0%) or conventional (49 out of 104; 47.1%) semen was used for fertilization. Moreover, the proportion of blastulation was similar ($P = 0.91$) in the sex-sorted semen group (19 out of 102; 18.6%) when compared with the conventional semen group (20 out of 104; 19.2%). In addition, the proportion of expanded blastocysts was similar ($P = 0.89$) in sex-sorted (16 out of 102; 15.6%) and conventional (17 out of 104; 16.3%) semen groups.

Discussion

To our knowledge, no studies have been published so far that include the use of sexed or conventional semen and the presence or absence of a CL as combined factors that may influence embryo production in vitro. These may be useful criteria

Table 1 Proportions of cleavage, compaction, blastulation, and expansion of blastocysts resulting from oocytes from ovaries with or without a corpus luteum and fertilized with conventional or sex-sorted semen

Corpus luteum on the ovary and type of semen used					
Parameter	CL+ sex-sorted	CL− sex-sorted	CL+ conventional	CL− conventional	*P* value
Cleavage	60/172 (34.9%)[c]	42/71 (59.1%)[b]	47/66 (71.2%)[b]	57/67 (85.1%)[a]	< 0.01
Compaction	29/60 (48.3%)[a]	21/42 (50.0%)[a]	21/47 (44.7%)[a]	28/57 (49.1%)[a]	0.95
Blastulation	8/60 (13.3%)[a]	11/42 (26.2%)[a]	5/47 (10.6%)[a]	15/57 (26.3%)[a]	0.12
Expansion of blastocysts	7/60 (11.7%)[a]	9/42 (21.4%)[a]	4/47 (8.5%)[a]	13/57 (22.8%)[a]	0.13

Different superscripts within the same row indicate differences ($P < 0.05$)

to consider in in vitro embryo production programs, given the fact that, currently, sexed semen is increasingly used and the search for more competent oocytes is constant. The increased rate of maturation of oocytes in the CL− group in the present study is consistent with results from Quezada-Casasola et al. (2018), who observed higher cumulus expansion in COCs from CL-absent ovaries. Discrepancies concerning the effect of the CL on oocyte developmental competence have been reported, as it has been proposed that as a CL is formed, the vascularity of the ovary increases and as this angiogenic process increases the blood flow, a proper amount of hormones and nutrients is available to the developing follicles, which increases oocyte quality (Penitente-Filho et al., 2014). Conversely, it has been reported that the new blood vessels formed for CL during its formation provide it with greater blood flow, which is needed for the subsequent progesterone synthesis, compared with other ovarian tissues, including follicles (Shabankareh et al., 2013). This decrease in blood reaching a developing follicle results in a decreased supply of pituitary gonadotropins and other substances needed for the proper development of the oocyte and the follicle. This mechanism may affect later egg maturation, as well as the subsequent embryonic developmental competence and quality (Acosta and Miyamoto, 2004). Another interesting mechanism that has been involved in the quality of the oocyte output is the one proposed by Contreras-Solis et al. (2008), who reported the existence of an intraovarian effect of the CL, with a greater decrease in the number of follicles reaching a large size in the ovary ipsilateral to that CL. These same results, which support those obtained by Bartlewski et al. in ewes (Bartlewski et al. 2001), indicate the existence of local inhibitory factors produced by the CL, rather than an effect of changes in gonadotrophin release similarly to inhibin, which is widely known to be secreted by the CL and to affect follicular size, growth rate, and oocyte competence (Shabankareh et al., 2015). A higher proportion of viable oocytes in the ovaries without a CL was also obtained by Peralta-Torres et al. (2017), who indicate that this was due to a better follicular environment as a result of a greater concentration of gonadotropins and other factors due to the lack of progesterone and inhibin secreted by the CL.

In relation to the potential paracrine effects that the CL can exert on the oocyte and the resulting embryo, receptors for both progesterone and estrogen have been found in cells from developing follicles (Özdemir and Çomaklı, 2018; Terzaghi et al., 2018). It is important to note that progesterone suppresses LH pulse frequency, which is critical for both follicle and oocyte development prior to maturation (Contreras-Solis et al., 2008). Interestingly, high progesterone levels are related to a decrease in estradiol production (Santos et al., 2009), whereas levels of this last hormone around final maturation time positively correlate with developmental competence (Heidari et al., 2019). Regarding cleavage of in vitro-inseminated oocytes, Rizos et al. (2002), Vassena et al. (2003), Sirard et al. (2006), and Mermillod et al. (2008) suggested that the capacity to attain the first mitotic division reflects

Table 2 Maturation, compaction, blastulation, and expansion rates resulting from bovine oocytes coming from ovaries with or without a corpus luteum

Corpus luteum on the ovary			
Parameter	Present (CL+)	Absent (CL−)	*P* value
Expansion of cumulus cells	217/238 (91.2%)[a]	136/138 (98.5%)[b]	< 0.01
Compaction	50/107 (46.7%)[a]	49/99 (49.4%)[a]	0.69
Blastulation	13/107 (12.1%)[a]	26/99 (26.2%)[b]	< 0.01
Expansion of blastocysts	11/107 (10.2%)[a]	22/99 (22.2%)[b]	0.01

Different superscripts within the same row indicate differences ($P < 0.05$)

Table 3 Compaction, blastulation, and expansion rates resulting from bovine oocytes fertilized with sex-sorted or conventional semen

Type of semen			
Parameter	Sex-sorted	Conventional	*P* value
Compaction	50/102 (49.0%)[b]	49/104 (47.1%)[b]	0.78
Blastulation	19/102 (18.6%)[b]	20/104 (19.2%)[b]	0.91
Expansion of blastocysts	16/102 (15.6%)[b]	17/104 (16.3%)[b]	0.89

Different superscripts within the same row indicate differences ($P < 0.05$)

the intrinsic competence acquired by the egg during folliculogenesis rather than the effect of in vitro culture. The increased cleavage rates observed in CL− oocytes support the idea that the oocyte developmental competence could be negatively affected, not only during maturation but also through fertilization, cleavage, and further development by the presence of a CL. In agreement, Hajarian et al. (2016) also detected higher cleavage following IVF of eggs obtained from ovaries where a CL was absent. Therefore, the suppressive effect of progesterone from the CL on the viability of dominant follicles suggested by Contreras-Solis et al. (2008) may also exert its actions throughout fertilization and embryonic development.

In the current study, it was found a surplus in blastocyst formation upon IVF of oocytes from the CL− group. This is coincident with previous research where a greater blastocyst rate was generated from eggs extracted from bovine ovaries lacking a CL (Shabankareh et al., 2015). It must be underscored that the ability of blastocysts to form, and subsequently expand in vitro within 7–8 days post-insemination, is a major factor to establish a pregnancy following transference in cattle (Kubisch et al., 2004; Hoelker et al., 2006; Peippo et al., 2011). As can be seen in results from the present study, blastulation and expansion rates generated by IVF of oocytes obtained from ovaries with a CL are lower than those from the CL− group. Such observation supports the idea that the capacity to sustain early embryonic development is influenced by the follicular status from which the oocyte is obtained, as described by Sirard et al. (2006) and Shabankareh et al. (2015). In this way, oocytes coming from follicles at the dominant phase that are under the influence of high concentrations of progesterone maintain their developmental potential within the non-ovulating follicle only for a few days. In contrast, oocytes from follicles at the plateau phase, which is the stage between dominance establishment and the pre-ovulatory period where progesterone concentration decreases sharply, show high competence to reach the blastocyst and expand (Sirard et al., 2006).

In the present study, similar proportions of compaction, blastulation, and expansion of blastocysts were observed when both types of semen were used, but a lower cleavage rate was observed with sex-sorted semen when it was used to fertilize oocytes from the CL+ group. The similar embryonic compaction, blastulation, and expansion of blastocysts rates obtained here, regardless of the type of semen for IVF, are in agreement with some authors indicating that there are no negative effects on blastulation after use of sex-sorted semen (Carvalho et al., 2010; Pontes et al., 2010). However, these observations are not consistent with other reports in *Bos taurus* in which lower amounts of embryos were obtained upon fertilization with sex-sorted semen (Stinshoff et al., 2012; Lopez et al., 2015). Previous reports indicate that stress produced by sperm sorting negatively affects mitochondrial activity in the spermatozoon, reducing its lifespan (Rath et al., 2013). Additionally, it has been reported that embryos produced by sorted spermatozoa may have impaired number of mitochondria, as well as structural defects of the nuclear envelope. Concerning this, it was found that such changes could compromise embryonic development (Palma et al., 2008). Moreover, Blondin et al. (2009) detected higher cleavage but lower blastocyst rates using sex-sorted semen. Although discrepancies in the results may be attributed to differences in IVF protocols (Blondin et al., 2009; Lopez et al., 2015), several strategies have been attempted to increase blastulation after fertilization with sexed semen, such as the increase of sperm cell concentration. Such strategy improved cleavage and blastocyst rates (Barceló-Fimbres et al., 2011). In this regard, it is important to note that the sexed semen straws used in the present study contained standard amounts of sperm. Furthermore, semen dilutions here provided the same sperm concentration in comparison to fertilization with conventional semen. This experimental condition and the fact that spermatozoa may undergo the damage described above due to sex sorting process, and even more, the unfavorable conditions of the oocytes from CL+ ovaries mentioned above contribute to the explanation of the low cleavage percentage in this experimental group in the present study.

In conclusion, the findings of the present study indicate that a CL in the ovary from which oocytes are obtained can compromise them as early as maturation and cleavage. Also, a higher proportion of cleavage-stage embryos can be obtained if conventional semen is used for fertilization of oocytes coming from ovaries without a CL.

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Compliance with ethical standards

All procedures in the present study complied with the ethical standards of the national and institutional guides on the care and use of laboratory animals in Mexico (NOM-051-ZOO-1995: Humanitarian care of animals during mobilization; NOM-033-ZOO-1995: Humanitarian slaughter of domestic and wild animals, as well as the institutional regulation of the Bioethics Committee of the Universidad Autónoma de Ciudad Juárez).

Conflict of interest The authors declare that they have no conflict of interest.

References

Acosta, T.J. and Miyamoto, A. 2004. Vascular control of ovarian function: ovulation, corpus luteum formation and regression. Animal Reproduction Science, 82-83, 127-140.

Aggag, M.A.M., Hashaad, A.Y.A., El-Khawagah, A.R.M., Kandiel, M.M.M. and Mahmoud, K.G.M. 2017. Assessment of the impact of corpus luteum on *in vitro* maturation and developmental competence of dromedary camel oocytes. Egyptian Journal of Veterinary Science, 48(1), 23-29.

Barceló-Fimbres, M., Campos-Chillon, L.F. and Seidel, G.E. 2011. In vitro fertilization using non-sexed and sexed bovine sperm: sperm concentration, sorter pressure, and bull effects. Reproduction in Domestic Animals, 46(3), 495-502.

Bartlewski, P.M., Beard, A.P. and Rawlings, N.C. 2001. Ultrasonographic study of the effects of the corpus luteum on antral follicular development in unilaterally ovulating western white-faced ewes. Animal Reproduction Science, 65(3-4), 231-244.

Blondin, P., Beaulieu, M., Fournier, V., Morin, N., Crawford, L., Madan, P. and King, W.A. 2009. Analysis of bovine sexed sperm for IVF from sorting to the embryo. Theriogenology, 71(1), 30-38.

Britt, J.H. 2008. Oocyte development in cattle: physiological and genetic aspects. Revista Brasileira de Zootecnia, 37 Suppl, 110-115.

Caixeta, E.S, Sutton-McDowall, M.L., Gilchrist, R.B., Thompson, J.G., Price, C.A., Machado, M.F., Lima, P.F. and Buratini, J. 2013. Bone morphogenetic protein 15 and fibroblast growth factor 10 enhance cumulus expansion, glucose uptake, and expression of genes in the ovulatory cascade during in vitro maturation of bovine cumulus-oocyte complexes. Reproduction, 146(1), 27-35.

Carvalho, J.O., Sartori, R., Machado, G.M., Mourão, G.B. and Dode, M.A. 2010. Quality assessment of bovine cryopreserved sperm after sexing by flow cytometry and their use in in vitro embryo production. Theriogenology, 74(9), 1521-1530.

Contreras-Solis, I., Diaz, T., Lopez, G., Caigua, A., Lopez-Sebastian, A. and Gonzalez-Bulnes, A. 2008. Systemic and intraovarian effects of corpus luteum on follicular dynamics during estrous cycle in hair breed sheep. Animal Reproduction Science, 104(1), 47-55.

Hajarian, H., Shahsavari, M.H., Karami-shabankareh, H. and Dashtizad, M. 2016. The presence of corpus luteum may have a negative impact on in vitro developmental competency of bovine oocytes. Reproductive Biology, 16(1), 47-52.

Heidari, M., Kafi, M., Mirzaei, A., Asaadi, A. and Mokhtari, A. 2019. Effects of follicular fluid of preovulatory follicles of repeat breeder dairy cows with subclinical endometritis on oocyte developmental competence. Animal Reproduction Science, 205, 62-69.

Hoelker, M., Schmoll, F., Schneider, H., Rings, F., Gilles, M., Tesfaye, D., Jennen, D., Tholen, E., Griese, J. and Schellander, K. 2006. Bovine blastocyst diameter as a morphological tool to predict embryo cell counts, embryo sex, hatching ability and developmental characteristics after transfer to recipients. Reproduction, Fertility and Development, 18(5), 551-557.

Islam, M.R., Khandoker, M.A.M.Y., Afroz, S., Rahman, M.G.M. and Khan, R.I. 2007. Qualitative and quantitative analysis of goat ovaries, follicles and oocytes in view of in vitro production embryos. Journal of Zhejiang University Science B, 8(7), 465-469.

Kastelic, J.P., Bergfelt, D.R. and Ginther, O.J.. 1990. Relationship between ultrasonic assessment of the corpus luteum and plasma progesterone concentration in heifers. Theriogenology 33(6), 1269-1278.

Kubisch, H.M., Sirisathien, S., Bosch, P., Hernandez-Fonseca, H.J., Clements, G., Liukkonen, J.R. and Brackett, B.G. 2004. Effects of developmental stage, embryonic interferon-tau secretion and recipient synchrony on pregnancy rate after transfer of in vitro produced bovine blastocysts. Reproduction in Domestic Animals, 39(2), 120-124.

Lopez, W.O., Alvis-Miranda, H.R., Gamarra, A.F., Rendon, B., Borda, D.A., Albicker, U., Fonoff, E.T. and Martinez-Diaz, M. 2015. Effects of sexed semen and interactive effects on commercial in vitro embryo production when oocytes are collected from cows of Bos indicus, and Bos taurus breeding and crossbred cows of these subspecies. Animal Reproduction Science, 156:58-63.

Lucy, M.C. 2001. Reproductive loss in high-producing dairy cattle: where will it end? Journal of Dairy Science, 84(6), 1277-1293.

Mermillod, P., Dalbiès-Tran, R., Uzbekova, S., Thélie, A., Traverso, J.M., Perreau, C., Papillier, P. and Monget, P. 2008. Factors affecting oocyte quality: who is driving the follicle? Reproduction in Domestic Animals, 43 Suppl 2, 393-400.

Özdemir, S. and Çomaklı, S. 2018. Investigation of the interaction between bta-miR-222 and the estrogen receptor alpha gene in the bovine ovarium. Reproductive Biology, 18(3), 259-266.

Palma, G.A. Olivier, N.S., Neumüller, Ch. and Sinowatz, F. 2008. Effects of sex-sorted spermatozoa on the efficiency of in vitro fertilization and ultrastructure of in vitro produced bovine blastocysts. Anatomia, Histologia, Embryologia, 37(1), 67-73.

Peippo, J., Machaty, Z. and Peter, A. 2011. Terminologies for the preattachment bovine embryo. Theriogenology, 76(8), 1373-1379.

Penitente-Filho, J.M., Carrascal, E., Oliveira, F.A., Zolini A.M., Oliveira, C.T., Costa, I.A. and Torres, C.A. 2014. Influence of dominant follicle and corpus luteum on recovery of good quality oocytes for in vitro embryo production in cattle. British Biotechnology Journal, 4(12), 1305-1312.

Penitente-Filho, J.M., Jimenez, C.R., Zolini, A.M., Carrascal, E., Azevedo, J.L., Silveira C.O., Oliveira F.A. and Torres, C.A. 2015. Influence of corpus luteum and ovarian volume on the number and quality of bovine oocytes. Animal Science Journal, 86(2), 148-152.

Peralta-Torres, J.A., Aké-López, J.R., Segura-Correa, J.C. and Aké-Villanueva, J.R. 2017. Effect of season on follicular population, quality and nuclear maturation of bovine oocytes under tropical conditions. Animal Reproduction Science, 87,47-53.

Pfeifer, L.F.M., Sartori, R., Pivato, I., Rumpf, R., Nogueira, G.P., Xavier, E.G., Dionello, N.J.L. and Corrêa, M.N. 2009. Effect of circulating progesterone on in vitro developmental competence of bovine oocytes. Animal Reproduction. 6(3), 473-480.

Pontes, J.H.F., Silva, K.C.F., Basso, A.C., Rigo, A.G., Ferreira, C.R., Santos, G.M.G., Sanches, B.V., Porcionato, J.P.F., Vieira, P.H.S., Faifer, F.S., Sterza, F.A.M., Schenk, J.L. and Seneda, M.M. 2010. Large-scale in vitro embryo production and pregnancy rates from Bos taurus, Bos indicus, and indicus-taurus dairy cows using sexed sperm. Theriogenology, 74(8), 1349-1355.

Quezada-Casasola, A., Martínez-Armendáriz, K.E., Itzá-Ortiz, M.F., Escárcega-Ávila, A.M., Pérez-Eguía, E., Filipiak, Y., Larocca, C. and Carrera-Chávez, J.M. 2018. Effect of presence of corpora lutea on cumulus expansion of in vitro matured bovine oocytes selected by trypan blue and brilliant cresyl blue tests. Journal of Applied Animal Research, 46(1), 967-972.

Rath, D., Barcikowski, S., de Graaf, S., Garrels, W., Grossfeld, R., Klein, S., Knabe, W., Knorr, C., Kues, W., Meyer, H., Michl, J., Moench-Tegeder, G., Rehbock, C., Taylor, U. and Washausen, S. 2013. Sex selection of sperm in farm animals: status report and developmental prospects. Reproduction, 145(1), R15-R30.

Rehman, N.U., Sarwar, M. and Samad, H.A. 2001. In vitro production of bovine embryos - a review. Asian-Australian Journal of Animal Sciences, 14(9), 1342-1351.

Rizos, D., Ward, F., Duffy, P., Boland, M.P. and Lonergan, P. 2002. Consequences of bovine oocyte maturation, fertilization or early embryo development in vitro versus in vivo: Implications for

blastocyst yield and blastocyst quality. Molecular Reproduction and Development, 61, 234-248.

Santos, J., Rutigliano, H. and Sá Filho, M. 2009. Risk factors for resumption of pospartum estrous cycles and embryonic survival in lactating dairy cows. Animal Reproduction Science, 110(3-4), 207-221.

Shabankareh, H.K., Kor, N.M. and Hajarian, H. 2013. The influence of the corpus luteum on metabolites composition of follicular fluid from different sized follicles and their relationship to serum concentrations in dairy cows. Animal Reproduction Science, 140(3-4), 109-114.

Shabankareh, H.K., Shahsavari, M.H., Hajarian, H. and Moghaddam, G. 2015. In vitro developmental competence of bovine oocytes: effect of corpus luteum and follicle size. Iranian Journal of Reproductive Medicine, 13(10), 615-622.

Shimada, M. and Terada, T. 2002. FSH and LH induce progesterone production and progesterone receptor synthesis in cumulus cells: a requirement for meiotic resumption in porcine oocytes. Molecular Human Reproduction, 8(7), 612-618.

Silva, C.C. and Knight, P.G. 2000. Effect of androgens, progesterone and their antagonist on the development competence of in vitro matured bovine oocytes. Journal of Reproduction and Fertility, 119(2), 261-269.

Sirard, M.A., Richard, F., Blondin, P. and Robert, C. 2006. Contribution of the oocyte to embryo quality. Theriogenology, 65(1), 126-136.

Stinshoff, H., Krienke, M., Ekhlasi-Hundrieser, M., Wilkening, S., Hanstedt, A., Frese, D., Rath, D., Bollwein, H. and Wrenzycki, C. 2012. Seminal plasma and seminal plasma proteins added to bulk sorted sperm do not alter the mRNA expression of in vitro produced bovine embryos. Theriogenology, 78(1), 132-139.

Stojkovic, M., Machado, S.A., Stojkovik, P., Zakhartchenko, V., Hutzler, P., Gonçalves, P.B. and Wolf, E. 2001. Mitochondrial distribution and adenosine triphosphate content of bovine oocytes before and after in vitro maturation: correlation with morphological criteria and developmental capacity after in vitro fertilization and culture. Biology of Reproduction, 64(3), 904-909.

Terzaghi, L., Luciano, A.M., Dall'Acqua, P.C., Modina, S.C., Peluso, J.J. and Lodde, V. 2018. PGRMC1 localization and putative function in the nucleolus of bovine granulosa cells and oocytes. Reproduction, 155(3), 273-282.

Vassena, R., Mapletoft, R.J., Allodi, S., Singh, J. and Adams, G.P. 2003. Morphology and development competence of bovine oocytes relative to follicular status. Theriogenology, 60(5), 923-932.

Zhang, K., Hansen, P.J. and Ealy, A.D. 2010. Fibroblast growth factor 10 enhances bovine oocyte maturation and developmental competence in vitro. Reproduction, 140(6), 815-826.

Zhang, K. and Smith, G.W. 2015. Maternal control of early embryogenesis in mammals. Reproduction, Fertility and Development, 27(6), 880-896.