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Oocyte origin affects the *in vitro* embryo production and development of Holstein (*Bos taurus taurus*) - Gyr (*Bos taurus indicus*) reciprocal cross embryos

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ABSTRACT

A reciprocal crossbred embryo production approach was used to assess effects of maternal breed on embryo development in tropical conditions (average temperature 22.0 °C and 77.9% relative humidity). Oocytes were recovered by ovum pick-up (OPU) from Gyr and Holstein donors (n = 90 Holstein and 83 Gyr OPUs). Female F1 embryos were produced by fertilization with sperm bearing X-chromosomes from Holstein semen (n = 615 Gyr oocytes) or Gyr semen (n = 255 Holstein oocytes). Blastocysts were transferred to recipients 168 h post-insemination (h.p.i.) (n = 70–144) and there were assessments of pregnancies until birth. Oocyte number per OPU (Gyr 10.0 ± 0.7 compared with Holstein 6.3 ± 0.4) and percentage viable oocytes (Gyr 78.8 ± 1.9% compared with Holstein 71.2 ± 2.2%) were less for Holstein donor animals. There was a 2.8 fold fewer total number of F1 blastocysts when Holstein donors were used (Gyr: 260, Holstein: 91). Pregnancy assessment during the different stages of gestation indicated the percentage pregnancy was less when embryos were produced from Holstein oocytes (Gyr and Holstein respectively: early pregnancy, 47.9% compared with 38.6%; mid-pregnancy, 44.4% compared with 31.4%; late pregnancy, 41.0% compared with 22.9%). Pregnancy length was also affected by maternal breed (Gyr: 280.8 ± 0.6, Holstein: 286.3 ± 0.7). It is concluded that in a tropical environment the maternal breed affects crossbred embryo development with pregnancy rates during the latter stages of gestation being greater when Gyr oocytes are used for production of embryos.

1. Introduction

Economic value of *Bos taurus taurus* - *Bos taurus indicus* F1 crosses is greater when there is comparison with other continuous

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breeding systems due to the larger milk yields and greater longevity of Holstein-Gyr cows (Girolando breed) commonly used for heterosis exploitation in tropical dairy herds (Madalena et al., 1990; Canaza-Cayo et al., 2016).

Animal breed from which oocytes are derived affects the capacity of IVF-derived embryos to develop. *Bos taurus taurus* as compared with *Bos taurus indicus* cattle have ovaries containing fewer antral follicles, a larger ovulatory follicle size and a greater metabolism rate. There is also a different hormonal profile in *Bos taurus taurus* as compared with *Bos taurus indicus* cattle. *Bos taurus taurus cows* have a lesser peak of circulating estradiol and progesterone concentrations than *Bos taurus indicus* (Sartori et al., 2016). These differences result in a greater hormone requirement for superovulation and artificial insemination in *Bos taurus taurus* compared with *Bos taurus indicus* cows (Soares et al., 2011) and can induce distinct responses to ovarian stimulation for oocyte recovery.

Bos taurus taurus and *Bos taurus indicus* cattle have physiological differences that might include an oocyte maternally inherited reserve of proteins. Maternal mRNA supports embryonic development until the time of activation of the embryonic genome, and even though this occurs early in mouse embryos (at 2-cell stage) (Moore, 1975), in other species embryonic genome activation (EGA) can occur later. In human embryos, EGA occurs at the 4–8 cell (Braude et al., 1988) and even later at the 8–16 cell stage in cattle (De Sousa et al., 1998) and sheep (Crosby et al., 1988). The primary period of initiation of embryonic genome transcription occurs at the 8–16 cell stage in cattle (Memili and First, 2000).

An important example of phenotypic differences as a result of breed are the maternal oocyte content that affects the sensitivity to thermal stress. *Bos taurus* taurus derived oocytes are more sensitive to thermal stress than *Bos taurus indicus* oocytes indicating there is a genetic effect on thermal stress (Paula-Lopes et al., 2013). Differences in the cleavage rates (de Armas et al., 1994) and development to the blastocyst stage between *Bos taurus Taurus-* and *Bos taurus indicus-derived* oocytes have also been reported (Fischer et al., 2000; Camargo et al., 2007) and this indicates there are differences in oocyte competence.

A relevant question though is whether there would be differences between F1 derived embryos produced by reciprocal crosses, because after EGA, F1 crossbred embryos would have a similar genetic composition. Even though there was no difference in blastocyst production and pregnancy rate when there was transfer of F1 embryos produced from Holstein or Gyr oocytes into recipients in a field study (Pontes et al., 2010), phenotypic dissimilarities such as length of gestation and birth weight between reciprocal crosses of *Bos taurus taurus* and *Bos taurus indicus* have been reported (Amen et al., 2007a). It, therefore, is possible that there are differences in these reciprocal crosses that affect development of preimplantation embryos.

In the present study, the aim was to compare the development of F1 embryos derived from Holstein (*Bos taurus taurus)* or Gyr (*Bos taurus indicus)* oocytes, and investigate the effectiveness of a protocol for synchronization of the timing of follicular wave development among animals in heat stress conditions (measured by temperature humidity index). Those two variables are important in affecting the outcomes when there is use of most IVF systems and, based on the previously published information, can affect *Bos taurus taurus* and *Bos taurus indicus* embryonic development in distinct ways. The hypothesis was that embryonic/fetal development would be affected by the reciprocal crossbred genome, as a result of the breed of the female from the oocytes were derived even after implantation, favoring the breed more adapted to tropical conditions. In the present study, therefore, there is a description and comparison of oocyte recovery, *in vitro* embryo production and post transfer embryonic/fetal development, providing a broad view of reciprocal F1 offspring production using IVF, and highlighting processes affected by maternal components of cattle embryology.

2. Materials and methods

2.1. Experimental design

A summary of the experimental design, including number of structures, replicates and statistical factors, is presented in Fig. 1. Gyr (n = 12) and Holstein (n = 13) oocyte donors were divided into two plots (six Gyr and six Holstein; six Gyr and seven Holstein) and cows of each plot were submitted to ovum pick-up (OPU) for 10 months, totaling 14 replicates (seven per plot). Recovered oocytes were counted and morphologically evaluated (Fig. 1.1). Viable oocytes were matured for production of reciprocal Gyr-Holstein crossbred embryos. Cleavage and blastocyst rate percentages were assessed. Sexed semen was used (Fig. 1.2). Day 7 Grade 1 blastocysts produced from Gyr or Holstein oocytes were randomly transferred to a homogeneous Girolando recipients and pregnancy rates were assessed 30 and 60 days after transfer and at expected time of parturition. Additional pregnancy data were obtained at the same experimental farm (Fig. 1.3). Pregnancy length of F1 fetuses produced with Gyr or Holstein oocytes was compared. Additional pregnancy data were obtained at the same experimental farm were included (Fig. 1.3 and Fig. 1.4). The THI and protocol for synchronization of timing of follicular wave development among animals were included as factors and associations were assessed for embryos from Gyr and Holstein cows using IVF assays. In six replicates (three per plot) hormonal synchronizations were performed and in eight replicates (four per plot) dominant follicle aspiration occurred. Four replicates (two per plot) were performed during the months when there was a greater THI and ten replicates (five per plor) were performed during months when there was a lesser THI.

2.2. Reagents

Reagents were purchased from Sigma Chemical Co. (St. Louis, MO), culture medium was purchased from Bioklone (Jaboticabal, Brazil) and hormones were purchased from Ourofino (Sertaozinho, Brazil), unless otherwise stated.

2.3. Animals and maintenance

Mean temperatures during this period were 22.0 ± 4.5 °C (min. 9.5 and max. 37.5 °C) and air relative humidity 77.8 ± 15.5%.

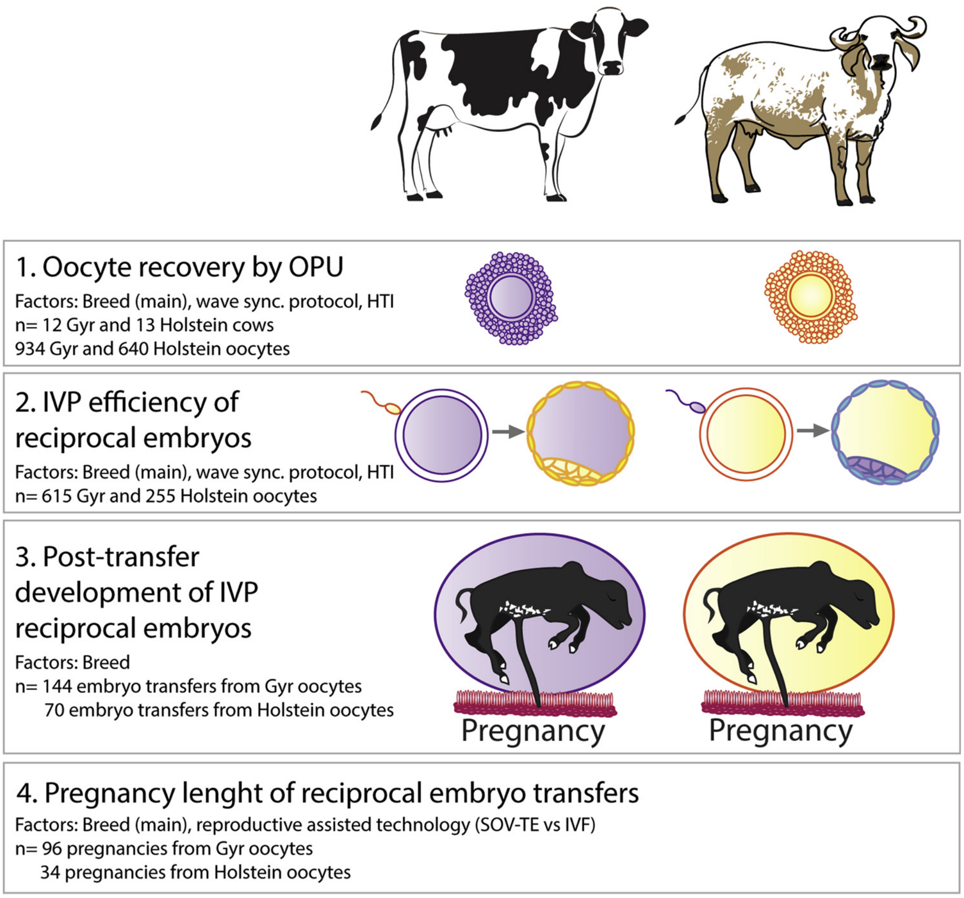

Fig. 1. Experimental Design; Developmental competence of reciprocal F1 crossbred embryos produced from oocytes of Gyr and Holstein cows; 1) Oocyte recovery after OPU; 2) *In vitro* fertilization (IVF) of Gyr oocytes with Holstein semen and Holstein oocytes with Gyr semen for production of reciprocal F1 embryos, Female embryos were studied, by using sorted semen, Percentage cleavage (d4) and blastocyst formation (d7) rates were compared; 3) Pregnancy rates for reciprocal F1 embryos transferred to crossbred recipients were assessed at 30 (early), 60 (mid-) and 270 (late) days after transfer; 4) Pregnancy length was assessed for IVF and SOV-TE gestations when there were reciprocal F1 embryo transfers.

(min. 19% and max. 97%). Twelve estrous cyclic non-lactating Gyr cows with an average body weight of 452 ± 63 kg and thirteen estrous cyclic non-lactating Holstein cows with an average body weight of 581 ± 79 kg were assigned to this experiment. Animals were maintained in the same pasture with mineral supplementation. Procedures followed ethical guidelines for animal experimentation and were approved by a local Animal Care and Use Committee (CEUA – EGL, protocol 23/2013).

2.4. Oocyte recovery

Ovum pick up (OPU) was performed with at least a 14 day interval between sessions. Stage of follicular wave development was synchronized using a 3 mg of norgestomet auricular implant (Crestar, Intervet), 2 mg estradiol benzoate and 150 μg D-cloprostenol 7 days before OPU (hormonal synchronization) or by dominant follicle aspiration 72 h prior to OPU. The same protocol was used for Gyr and Holstein donors in each replicate. The OPU procedure was conducted as previously described (Oliveira et al., 2017). Recovered cumulus-oocyte complexes were counted and classified. Morphologic classification of oocyte viability was based on a compact non-atretic cumulus with at least one layer of cells and a homogeneous cytoplasm or cytoplasm with a few granules.

2.5. Embryo production

Embryo production was performed as previously described (Oliveira et al., 2017). All procedures were conducted in oil-covered micro-drops of medium at 38.5 °C in an atmosphere of 5% CO_2 in air under saturated humidity. Briefly, oocytes were matured in 10% FCS TCM-199 supplemented with FSH, hCG and estradiol. Fertilization was performed in 0.6% BSA TALP-IVF supplemented with heparin, penicillamine, hypotaurine and epinephrine. Frozen-thawed semen from Gyr or Holstein bulls containing X-chromosome bearing spermatozoa sorted by flow cytometry (CRV Lagoa/ Sexing Technologies, Sertaozinho, Brazil) were used. The Gyr oocytes were fertilized with Holstein semen and Holstein oocytes were fertilized with Gyr semen. The same Holstein or Gyr bull previously tested for IVF with similar cleavage rates were used during all experiments. Flow cytometric sperm sorting based on differences in the DNA content is the usual method for separation of X- and Y-chromosome bearing spermatozoa, and its accuracy is about 90% (Seidel, 1999; Hamano, 2007). Each straw was centrifuged separately on a discontinuous 45/90 Percoll gradient for 7 min at 3600 x *g* and the pellet was washed in TALP-IVF and again centrifuged for 5 min at 520 x *g*. After centrifugation, the contents of the pellet were diluted and a final concentration of approximately 10^4 spermatozoa was used for each oocyte and gametes were co-cultured for 20 h. Presumptive zygotes were partially denuded of cumulus cells by vigorous pipetting and cultured in synthetic oviductal fluid (SOF) medium supplemented with 2.5% FCS and 6 mg/mL BSA. Remaining cumulus cells attached to the plastic surface and formed a monolayer of granulosa cells. Half of the medium was replaced at 96 and 144 h post-insemination. Cleavage rate was assessed at 96 and blastocyst rate at 168 h post-insemination.

2.6. Embryo transfer and pregnancy assessment

Embryos with a defined blastocoel at Day 7 (168 h.p.i.) ranging from small to expanded blastocysts were selected for transfer to homogeneous Girolando heifers. Recipients were treated with a vaginal progesterone device containing 1 mg, and with 2 mg estradiol benzoate. Heifers were administered a cloprostenol injection (0.5 mg) and estradiol cypionate (Zoetis, Parsippany, NJ) after 7 days when the progesterone device was removed. Embryo transfer was performed 9 days after removal of the progesterone device in recipients with a corpus luteum and adequate uterine tone. Embryos produced from Gyr or Holstein oocytes were randomly allocated to recipients. After embryo transfer, pregnancy was assessed by ultrasonic evaluation from days 28 to 35 after transfer (early pregnancy) and from days 55 to 65 after transfer (mid-pregnancy), and at the expected time of parturition and by birth of a healthy calf (late pregnancy, approximately 285 days).

Pregnancy length was calculated as the period between transfer and calving, plus 7 days. Additional observations for IVF embryos and for embryos produced by superovulation and embryo transfer (SOV-ET) produced in similar conditions were included in this analysis. Only female fetuses were analyzed.

2.7. Temperature and humidity assessment

During the experiment, temperature and humidity variables were assessed hourly and temperature and humidity index (THI) was calculated as described by the NRC (1971): THI = (1.8 x Tdb + 32) – [(0.55 – 0.0055 x RH) x (1.8 x tdb – 26.8)]. There was analysis each month of the experiment and categorization into High or Low THI as follows. High THI: mild stress (THI 72–79) present for more than 24 days, moderate stress (THI > 79) present for more than 2 days, THI < 55 absent. Low THI: mild stress (THI 72–79) present for less than 17 days, moderate stress (THI > 79) absent, and THI < 55 present for more than 10 days.

2.8. Statistical analysis

Statistical analysis was performed using the Minitab 18 software. For each animal OPU, total oocyte number, viable oocyte percentage rate, percentage cleavage rate, percentage blastocyst rate and blastocyst number was generated, totaling 83 Gyr and 90 Holstein records. Box-cox transformed values were compared between groups using an ANOVA. Breed (Gyr or Holstein), follicular wave synchronization protocol (hormone or dominant follicle aspiration) and THI classification (high or low) were included as fixed factors in the analysis. Interactions among factors were calculated.

Pregnancy rate was analyzed using the Fisher's Exact Test. For pregnancy length, breed (Gyr or Holstein) and assisted reproductive technology (IVF or SOV-TE) were included as fixed factors in the analysis and interaction between factors was calculated. Means were compared using an ANOVA. Linear regression was used for estimating the effect of viable oocyte, cleavage and blastocyst rates (predictor variables) over cleavage, blastocyst, early pregnancy and late pregnancy rates (outcome variables) in Gyr and Holstein oocytes separately. A 5% significance level was used for all analyses. Means are presented as the absolute mean, not the transformed mean.

3. Results

3.1. Temperature and humidity index (THI)

Mean temperature during the experiment was 22.0 °C (max. 37.5 °C, min. 9.5 °C) and mean relative humidity was 77.8% (max. 97%, min. 19%). Number of days when there was each of three THI classes during the experiment are depicted in Supplementary Fig. 1.

According to the classification described in the Materials and methods section of this manuscript, February, March, April, October and November were classified as "High THI" conditions and May, June, July and August were classified as "Low THI" conditions.

3.2. Oocyte recovery from Gyr and Holstein cows

First, there was comparison of results of data from Gyr and Holstein cows as oocyte donors when there was high or low THI conditions, using dominant follicle aspiration or hormonal treatment for follicular wave synchronization. There was collection of individual oocytes in 173 OPUs (n = 83 Gyr and 90 Holstein) obtained from 21 cows (n = 9 Gyr and 12 Holstein) during a 10 month

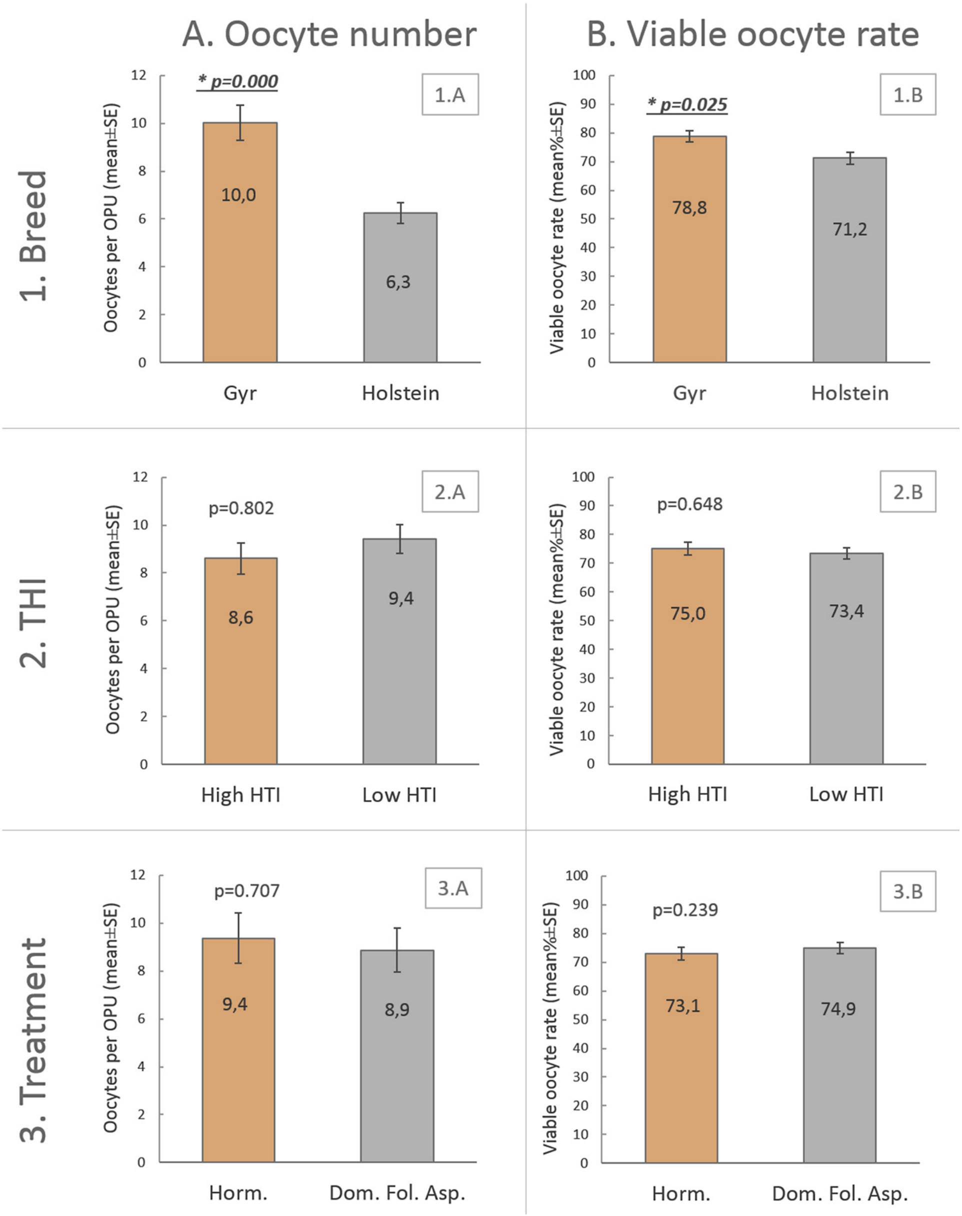

Fig. 2. Oocyte recovery after Gyr and Holstein OPU; Graphs depict mean oocyte number (A) and mean percentage of viable oocytes (B) per OPU session for 1 breed as the main factor, n = 934-640 oocytes per group, 83–90 observations); 2 - THI, n = 585–989 oocytes per group, 68–105 observations) and 3 - treatment, n = 834-740 oocytes per group, 94-79 observations); Asterisks indicate statistical difference.

period. When there was less than two oocytes collected from a donor, these data were excluded from the analysis. There was no interaction for breed, THI and estrous synchronization protocol factors for total oocyte or viable oocyte collection responses and results are presented independently.

Breed affected OPU results. A greater ($P < 0.05$) number of oocytes was recovered from Gyr compared with Holstein donors (Fig. 2.1.A). The percentage of viable oocytes (compact nonatretic cumulus with at least one layer of cumulus cells and a homogeneous cytoplasm) was also greater ($P < 0.05$) for Gyr donors (Fig. 2.1.B).

The THI did not affect OPU results. There was a similar ($P > 0.05$) oocyte number (Fig. 2.2.A) and viable oocyte rate (Fig. 2.2.B) for High or Low THI months. For follicular wave synchronization, there was no significant difference ($P > 0.05$) in oocyte number (Fig. 2.3.A) or percentage viable oocyte rate (Fig. 2.3.B) when hormonal treatment or dominant follicle aspiration was used.

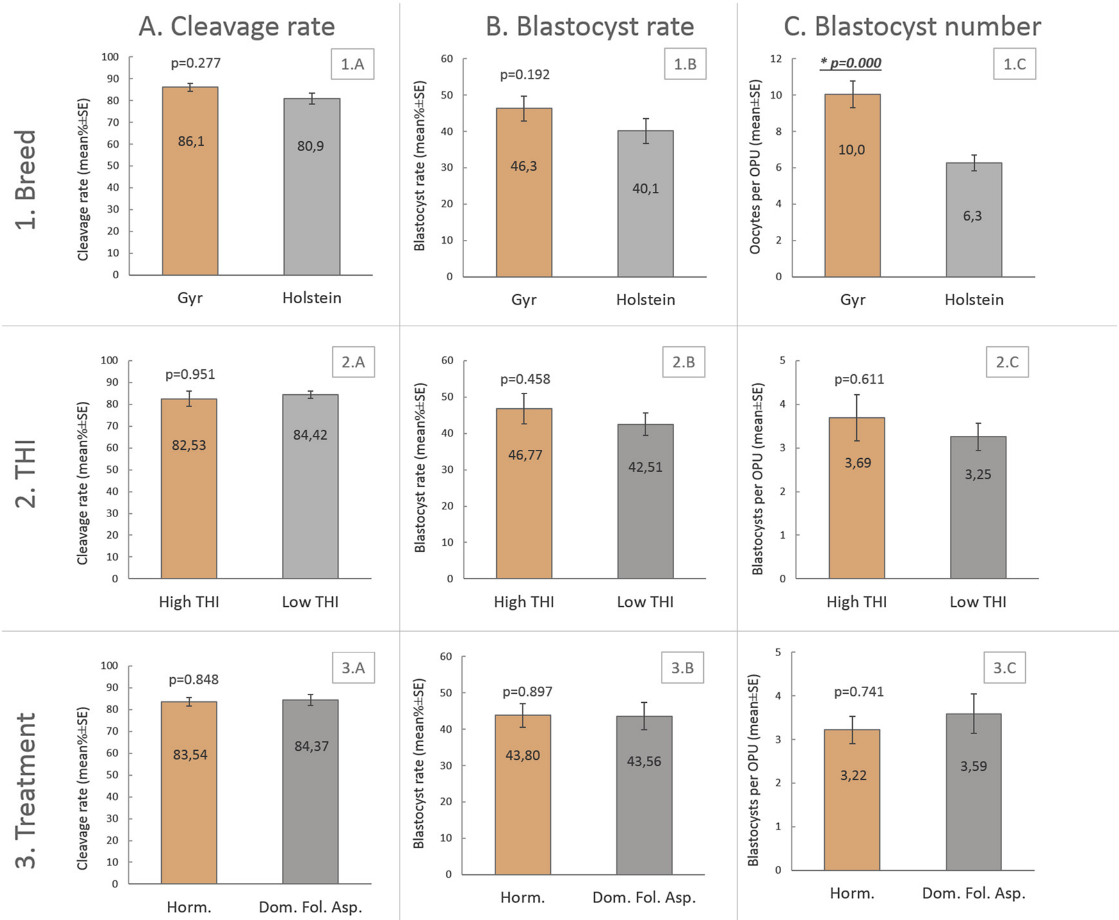

Fig. 3. Development of F1 embryos produced from Gyr or Holstein oocytes; Graphs depict percentage cleavage rate (A) blastocyst development rate (calculated from number of cleaved embryos); (B) blastocyst number per OPU session; and (C) for oocyte breed; 1 - main factor, n = 615-255 oocytes per group, 60-44 observations; THI 2 - n = 256–614 oocytes per group, 29–75 observations); and treatment 3 - n = 491-379 oocytes per group, 60-44 observations); Asterisks indicate statistical difference.

3.3. Embryo development of reciprocal F1 embryos

The IVF procedure was conducted for blastocyst production to address if oocytes factors (breed, THI, or synchronization protocol) to determine if there was an effect on development of F1 crossbred embryos. Data were only analyzed when there were collections containing more than four oocytes, to prevent extreme positive or extreme negative results in blastocyst rates (n = 615 Gyr and 255 Holstein oocytes, obtained in 60 Gyr and 44 Holstein OPU sessions). Reciprocal embryos were produced. No interaction ($P > 0.05$) was detected for breed, THI and estrous synchronization protocol factors for percent cleavage rate, percent blastocyst rate or blastocyst number responses, and results are presented independently. Mean percentage cleavage rate and blastocyst rate are depicted in Fig. 3.

Zygotes produced from Gyr or Holstein oocytes had a similar ($P > 0.05$) percentage cleavage rate (Fig. 3.1.A) and similar ($P > 0.05$) percentage blastocyst development rate (Fig. 3.1.B). Mean blastocyst number per OPU, however, was greater ($P < 0.05$) for embryos produced from Gyr oocytes (Fig. 3.1.C).

The THI did not affect ($P > 0.05$) percentage cleavage rate (Fig. 3.2.A), percentage blastocyst development rate (Fig. 3.2.B) or blastocyst number (Fig. 3.2.C). Percentage cleavage rate (Fig. 3.3.A), percentage blastocyst development rate (Fig. 3.3.B) and blastocyst number (Fig. 3.3.C) was not affected ($P > 0.05$) by type of protocol used to collect oocytes (hormonal compared with dominant follicle aspiration).

3.4. Post-transfer development of reciprocal F1 embryos

There was analysis of 214 (n = 70–144 per group) of Day 7 IVF blastocysts. For embryos produced from Gyr oocytes, there were data for eight Gyr donors and four Holstein bulls and for embryos produced from Holstein oocytes, ten Holstein donors and two Gyr bulls. Pregnancy was assessed at 30, 60 and 270 days after embryo transfer. Data were not analyzed for THI and estrous

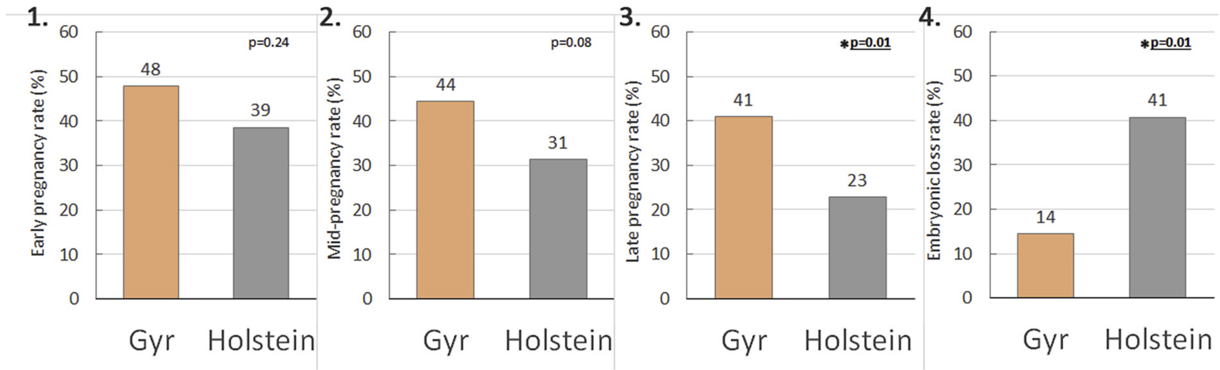

Fig. 4. Pregnancy rates after transfer of F1 embryos produced from Gyr or Holstein oocytes; Early pregnancy 1–30 days after transfer); mid-pregnancy 2–60 days after transfer); late pregnancy 3 - day of parturition); and embryonic loss 4 - rates are depicted (n = 144-70 embryo transfers per group); Asterisks indicate statistical difference between groups.

synchronization protocol due to the small number of replicates and because those factors were not significant with the previous analysis utilized to assess the data. In Fig. 4, there is depiction of the early (Fig. 4.1), mid- (Fig. 4.2) and late (Fig. 4.3) pregnancy rate percentage data. Embryos produced from Gyr oocytes had a greater ($P < 0.05$) late percentage pregnancy rate compared to embryos produced from Holstein oocytes. There were pregnancy losses in both groups but this was 2.9 fold greater ($P < 0.05$) when Holstein oocytes were transferred (Fig. 4.4).

Pregnancy length of F1 fetuses produced from Gyr or Holstein oocytes was also analyzed. Due to the small number of complete gestations in the experiment ($n = 26$), there was expansion of the dataset by including pregnancy records from the Embrapa Dairy Cattle Experimental Station for embryos produced in the same field conditions. Besides IVF embryos ($n = 96$), SOV embryos ($n = 34$) were also included and compared to address if the assisted reproductive technology would affect pregnancy length in conditions where the present study was conducted. Only female fetus pregnancies were analyzed. For embryos produced from Gyr oocytes, 23 Gyr donors and 15 Holstein bulls were used, and for embryos produced from Holstein oocytes, 15 Holstein donors and six Gyr bulls were used. The assisted reproductive technology (IVF/ SOV-TE) factor did not interact with breed factor ($P = 0.983$) and results are presented independently. Pregnancy length was estimated as 286.2 ± 0.7 days for embryos produced from Holstein oocytes and 280.4 ± 0.6 days for embryos produced from Gyr oocytes, 5.8 days longer ($P < 0.05$) when Holstein oocytes were used (Fig. 5.1). The factor of IVF/SOV-TE did not affect ($P > 0.05$) pregnancy length (Fig. 5.2).

3.5. Linear regression analysis for predictor variables

There was analysis of the correlation between potential predictor variables including percentage viable oocyte rate, cleavage rate, blastocyst rate, early pregnancy rate and late pregnancy rate. Linear regression analysis data indicated that the viable oocyte rate did not ($P > 0.05$) affect percentage cleavage, blastocyst development, early pregnancy or late pregnancy rates for either the Gyr or Holstein breeds (Table 1). Percentage cleavage rate affected ($P < 0.05$) percentage blastocyst development in embryos derived from both Gyr and Holstein oocytes. Percentage blastocyst development did not affect ($P > 0.05$) percentage early pregnancy in both groups, but late pregnancy was affected ($P < 0.05$) by percentage blastocyst development in embryos produced from Holstein oocytes

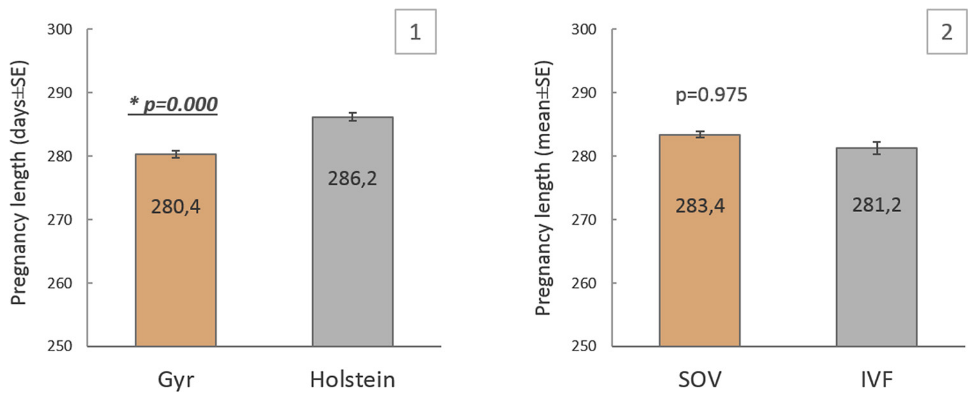

Fig. 5. Pregnancy length of F1 embryos produced from Gyr or Holstein oocytes; Mean pregnancy length for oocyte breed 1 - main factor, n = 96-34 per group; and assisted reproductive technology (IVF/SOV-TE) factor 2 - n = 91-39 per group) are depicted; Asterisks indicate statistical difference between groups.

Table 1
Linear regression analysis among potential predictor and outcome variables for embryos derived from Gyr (G) or Holstein (H) oocytes.

Predictor variable	Outcome Variable	R^2	P
Viable oocyte (G)	Cleavage	0.004	0.618
	Blastocyst	0.001	0.848
	Early pregnancy	0.001	0.802
	Late pregnancy	0.001	0.840
Viable oocyte (H)	Cleavage	0.007	0.555
	Blastocyst	0.010	0.593
	Early pregnancy	0.015	0.501
	Late pregnancy	0.108	0.231
Cleavage (G)	Blastocyst	0.184	**< 0.001**
Cleavage (H)	Blastocyst	0.214	**< 0.001**
Blastocyst (G)	Early pregnancy	0.001	0.805
	Late pregnancy	0.007	0.655
Blastocyst (H)	Early pregnancy	0.021	0.426
	Late pregnancy	0.399	**0.012**

(Table 1).

4. Discussion

A reciprocal embryo transfer experiment was used in the present study to assess the importance of maternal contribution for embryo/fetal development. Differences related to oocyte source on survivability were only evident during post transfer embryo/fetal development with the Gyr *(Bos taurus indicus)* oocytes affecting conceptus development post transfer in tropical conditions.

Oocyte quality was the first indication of differences as a result of breed of cow from which oocytes were obtained, possibly affecting all other developmental aspects that occur during gestation. Beyond the small number of recovered oocytes, there was a lesser quality (estimated by viable oocytes rate) for Holstein as compared with Gyr cumulus oocyte complexes in the present study. In addition, data from the regression analysis indicate percentage of blastocyst development affected late pregnancy percentages of donors for Holstein oocyte-derived embryos but not Gyr oocyte-derived embryos. Because both percentage of blastocyst development and pregnancy rates are affected by oocyte quality, this association indicates oocyte quality was less for Holstein oocytes in the present study.

Increased competence of *Bos taurus taurus* oocytes compared to *Bos taurus indicus* was described in countries with more temperate environments (Fischer et al., 2000), but in tropical conditions the opposite occurred in the present study. The THI (High or Low) did not affect any of variables evaluated in Gyr or Holstein oocytes, but there was mild heat stress (72–79 THI) (Armstrong, 1994) when the THI classifications of High and Low prevailed in the present study. These results indicate that mild heat stress can have adverse effects on *Bos taurus taurus* but not *Bos taurus indicus* oocytes. Rocha et al. (1998) also reported that high environmental temperatures and humidity resulted in a marked decrease in the quality of oocytes obtained from *Bos taurus taurus* cows, and there was a subsequent decrease in embryonic developmental capacity in *in vitro* culture conditions. Heat stress can activate intracellular biological processes that allow for adaptation or, promote death of affected structures, and this process appears to affect taurine oocytes to a greater extent than those from *Bos indicus* cattle (Camargo et al., 2007). There were previous results where there was a lesser percentage cleavage rate for embryos derived from Holstein oocytes and decreased percentage of embryos developing to the 8 to 16 cell and blastocyst stages (Camargo et al., 2007).

The F1 embryos developing from Holstein oocytes inherit cytoplasmic components including proteins and transcription factors from *Bos taurus taurus* which will regulate embryonic development until the time of genome activation. Heat stress can modify these components in a distinct way in *Bos taurus taurus* and *Bos taurus indicus* oocytes (Paula-Lopes et al., 2013) with *Bos taurus indicus* oocytes being less sensitive to heat stress and have a greater developmental capacity after IVF (Camargo et al., 2007).

Data from the present study highlights the importance of oocyte quality in post-implantation development because there were developmental effects after embryo transfer. Embryo developmental programming as a result of a stressor(s) of the maternal system during pregnancy has been described (Reynolds et al., 2010). In the present study there were effects of oocyte origin on fetal development. Increased fetal loss is related to ovarian hormonal stimulation in mice, another noted example of oocyte quality altering fetal development (Van der Auwera and D'Hooghe, 2001). Findings in the present study confirm that oocyte origin affects embryo development for a much longer period than expected, even in embryos with similar genetic composition, and this condition can affect embryonic production.

Likewise, gestation length of reciprocal F1 embryos differed, being similar to that of the maternal breed (longer for Holsteins than Gyrs). Differences were reported in fetal development after reciprocal Brahman and Simmental crosses, and a genomic imprinting was suggested as a possible cause (Dillon et al., 2015). Amen et al. (2007b) also reported that there were differential outcomes with the transfer of reciprocal F1 embryos, including differences in gestation length.

In conclusion, in the present study Gyr-Holstein F1 embryo production in tropical conditions was more efficient when there was use of oocytes from Gyr than Holstein cows, mainly due to (i) a greater oocyte yield, (ii) increased oocyte quality, and (iii) increased pregnancy rates. Results indicate oocyte origin affects the survival capacity of embryos/fetuses during post implantation development.

Declaration of Competing Interest

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us. We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property. We further confirm that any aspect of the work covered in this manuscript that has involved either experimental animals or human patients has been conducted with the ethical approval of all relevant bodies and that such approvals are acknowledged within the manuscript.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.anireprosci.2019.106165.

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