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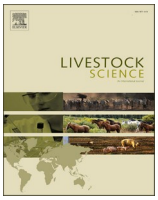

Parent-of-origin effects for the number of oocytes and embryos in Gir cattle

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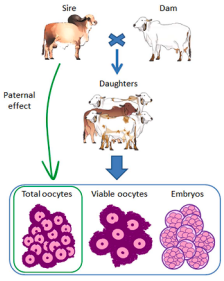
HIGHLIGHTS

- There is paternal effect for the number of total oocytes.
- Paternal effects explained 6 % of the phenotypic variance for total oocytes.
- No parental effects were observed for viable oocytes and embryos.
- Partial effects may still exist for the number of oocytes and embryos.

GRAPHICAL ABSTRACT



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ABSTRACT

Imprinting is a phenomenon that alters the expression of genes according to the parental origin of their alleles. A quantitative form to evaluate the imprinting effect is known as parent-of-origin effect. Our aim with this work is to identify parent-of-origin effects that influence the number of oocytes and embryos in Gir dairy cattle. A dataset with 17,526 Ovum Pick Up observations from 1641 Gir donors was used to estimate parent-of-origin effects for the traits number of total oocytes (TO), number of viable oocytes (VO) and number of embryos (EM). To identify parent-of-origin effects, dam and sire gametic effects were included, individually or together, in an animal model for TO, VO and EM traits. For TO, inclusion of paternal origin effects in the model was significant ($P < 0.05$), and explained 6 % of the total phenotypic variance. For VO and EM no significant parent-of-origin effects were found for either parental line. In conclusion, paternal effects appear to influence the total oocyte production in the Gir cattle breed.

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1. Introduction

Parent-of-origin effects occur when the expression level of an allele depends on parental inheritance (Lawson et al., 2013). Although several factors can cause parent-of-origin effects, genomic imprinting, which arises due to DNA-modifications during the gametogenesis process, is the best characterized (Blunk et al., 2017a, 2019). Imprinting is an epigenetic process that involves complete or partial inactivation of a gene inherited from one parent while its homologous gene inherited from the other parent is expressed (Hitchcock and Gardner, 2019). Although parent-of-origin effects plays a critical role in a variety of biological processes, including agricultural important traits, its effects are not commonly included in animal breeding programs (Blunk et al., 2017b; Lawson et al., 2013). Tier and Meyer (2012) mentioned that the lack of inclusion of parent-of-origin effects in breeding programs may result in biased estimated breeding values and genetic parameters. Given the importance of these effects, in the past years, analyses to identify them have been widely explored in several species, such as Arabidopsis (Hornslien et al., 2019), humans (Pilvar et al., 2019), sheep (Amiri Roudbar et al., 2018, 2017), goat (Mokhtari et al., 2022), horses (Perdomo-González et al., 2023), cattle (Blunk et al., 2019; Tier and Meyer, 2012), and swine (Neugebauer et al., 2010a). Using a genomic approach, Jiang et al. (2017) found significant contributions of imprinting effects for production and reproduction traits in the Holstein breed and indicated that imprinting effects contribute proportionally more to reproduction traits than to production traits. Using a quantitative approach, Amiri Roudbar et al. (2018) found parent-of-origin effect for reproductive traits in sheep. Some of the studies mentioned above worked from a quantitative perspective, identifying parent-of-origin effects based on phenotype data and statistical models (Amiri Roudbar et al., 2018, 2017; Mokhtari et al., 2022; Neugebauer et al., 2010a; Perdomo-González et al., 2023; Tier and Meyer, 2012), while other studies used a genomic approach, identifying imprinting patterns in genomic regions (Blunk et al., 2019; Hornslien et al., 2019; Jiang et al., 2017; Pilvar et al., 2019).

In the review made by Li and Li (2019) it is notable that the study of embryo development had a significant contribution to the discovery of genomic imprinting. They mention that, according to nuclear transfer experiments, it is highly probable that genomic imprinting of parental genomes plays a crucial role in ensuring complete embryonic development. Likewise, maternal and paternal imprinting was also discovered to affect oocyte growth in mice (Hiura et al., 2006; Joh et al., 2018). The importance of studying embryo and oocyte-related traits, especially in cattle, comes from the rising embryo industry, which reached over one million *in vitro*-produced (IVP) bovine embryos worldwide in 2021 (Viana, 2022). Furthermore, the successful embryogenesis process depends on oocyte growth and development (Walker and Biase, 2020), making it important to also study oocyte-related traits and its viability.

In recent years, studies have emerged exploring genetic and genomic aspects of traits related to oocyte and embryo production in cattle breeds (Jaton et al., 2020; Parker Gaddis et al., 2017; Perez et al., 2016; Rocha et al., 2022). For example, the Gir cattle, a breed originating from India, is also known for its resilience against high temperatures and parasites, and stands out as an exceptionally productive indicine breed for milk production in tropical regions such as Brazil (Panetto et al., 2021). *Bos indicus* breeds produce twice the oocyte production in comparison to *Bos taurus* cattle, demonstrating their potential for *in vitro* embryo production (Rotar and Souza, 2019). The Gir breed, as a *Bos primigenius indicus*, has been recognized for its utilization in reproductive technologies, achieving superior oocyte quality when compared to *Bos primigenius taurus*. This distinction has enabled the Gir breed to outperform taurine animals in terms of *in vitro* embryo production.

In our previous study (Rocha et al., 2022), we estimated variance components and genetic parameters for the number of viable oocytes, the number of total oocytes and the number of embryos, using an animal model based on repeatability and random regression approaches. However, considering the importance of oocyte and embryo-related traits for livestock production, there is a lack of studies estimating parent-of-origin effects related to the number of oocytes and embryos in cattle. Therefore, complementing our previous research (Rocha et al., 2022), our hypothesis in the current study is that parent-of-origin effects may affect oocyte and embryo production in Gir dairy cattle. Our aim with this study is to identify parent-of-origin effects that influence the number of oocytes and embryos in Gir dairy cattle.

2. Material and methods

2.1. Data structure

A dataset with 17,526 Ovum Pick Up (OPU) observations from 1641 Gir donors previously described by Rocha et al. (2022) was used. The dataset came from five commercial farms including the following traits: the number of viable oocytes (VO), the number of total oocytes (TO), and the number of embryos (EM). The collected oocytes were sent to the lab for quantification of viable and non-viable oocytes. Viable oocytes were fertilized in the *in vitro* fertilization (IVF) process. The EM trait is related to the total number of embryos produced after IVF, regardless of their quality or stage of development. For quality control, the following criteria were applied for sample exclusion: donors without correct identification, pooled donor samples, donors from other breeds, duplicate data and samples in which the number of embryos was greater than the number of total oocytes. Donors out of the age range between 1 and 16 years were excluded, because they were represented by very few observations. Only records from cows with at least three observations were considered. Descriptive statistics for the traits after quality control are available in Table 1.

The OPU sessions were performed from 2005 to 2020 in four seasons: (1) January–March; (2) April–June; (3) July–September; (4) October–December. The farms hired different companies to carry out the processes ranging from Ovum Pick Up to *in vitro* fertilization (OPU–IVF). In some cases, one farm hired more than one company to carry out these processes. Each company has its own protocol for OPU, IVF and other laboratory processes. In total, eight OPU-IVF protocols were applied varying among farms and in a few cases within farms. The number of OPU sessions ranged from 3 to 70 per donor, with a mean (standard deviation) of 10.68 (8.91). The interval (in days) between OPU sessions for each animal had a mean (standard deviation) of 97.01 (171.10). A minimum of 0 days for OPU interval indicated that two samples of the OPU session from the same cow on the same day were obtained and sent to the lab to be fertilized with semen from different bulls. The maximum OPU interval was 2570 days. Donor's age ranged from 1 to 16 years, with a mean (standard deviation) of 6.27 (3.19).

Animals were separated into 138 contemporary groups (CG) composed according to year, season, farm and OPU/*In Vitro* Fertilization protocol. A total of 238 bulls (Gir = 84 or Holstein = 154) were used for the *in vitro* fertilization processes. The frequency of use of these bulls ranged from 1 to 1789 samples, with an average of 73 samples per bull.

Table 1
Descriptive statistics[A] for the number of viable oocytes (VO), number of total oocytes (TO), and number of embryos (EM).

Traits	*N*	Mean	SD	MIN	MAX	CV
VO	17,524	15.82	12.89	0	182	81.46
TO	17,526	21.66	16.10	0	197	74.33
EM	17,498	2.94	3.70	0	46	125.66

[A] ***N***: number of data samples; **SD**: standard deviation; **MIN**: minimum; **MAX**: maximum; **CV**: coefficient of variation. Source: Adapted from Rocha et al. (2022) to include only the traits.

2.2. Gametic relationship matrix

The pedigree of the 1641 donors included 127 sires and 771 dams, with a total of 4679 animals covering up to 15 generations. Some of these Gir sires have semen samples available for purchase through commercial sire summaries, so several farms may have access to some of the same sires for reproduction purposes. A pedigree-based inbreeding was calculated with the "pedigree" package (Coster, 2012) using the R software (R Core Team, 2023 – R version 4.0.2; R Foundation for Statistical Computing, Vienna, Austria). Average inbreeding for the whole population was 0.015 and average inbreeding for the donors was 0.017. Additional details for the pedigree are available in Table 2.

To estimate the parent-of-origin effects, the gametic relationship matrix approach was used. This matrix was obtained from the gametic pedigree, which in turn was obtained from the animals' original pedigree file (Tier and Meyer, 2012). Then, the inverse of the genetic relationship matrix (Schaeffer et al., 1989) was obtained using the GGRinv program (Reinsch, 2020).

2.3. Parent-of-origin effects

Traits were transformed using the logarithmic scale: ln $(X + 1)$, where ln is the natural logarithm and X is the raw data (oocyte and embryos). The normal distribution of the residuals was verified by the Anderson–Darling test (Stephens, 1986; Thode, 2002). The animal model was defined in one of our previous studies (Rocha et al., 2022). In brief, analysis of variance was carried out to test for the significance of the effects (Table 3). After that, several models were tested for each trait and compared using Log Likelihood and Akaike Information Criterion values to choose the model with the best fit.

In the current study, paternal and maternal gametic effects were included in the animal model previously defined. Single-trait models were used to estimate paternal and/or maternal effects on the traits:

Animal model (Am) – no parental effect:

$$y = X\beta + Z_a a + \wp + e$$

Animal + Dam gametic effect model (ADm):

$$y = X\beta + Z_a a + Z_d g_d + \wp + e$$

Animal + Sire gametic effect model (ASm):

$$y = X\beta + Z_a a + Z_s g_s + \wp + e$$

Animal + Dam gametic effect + Sire gametic effect model (ADSm):

$$y = X\beta + Z_a a + Z_d g_d + Z_s g_s + \wp + e$$

where, $\boldsymbol{y}$, $\boldsymbol{\beta}$, $\boldsymbol{a}$, g_d, g_s, $\boldsymbol{p}$, and $\boldsymbol{e}$ are the vectors of observations, fixed effects, additive genetic random effects, dam gametic random effects, sire gametic random effects, permanent environmental random effects and residual effects, respectively; $\boldsymbol{X}$, $\boldsymbol{Z}$, and $\boldsymbol{W}$ are the incidence matrices of fixed and random effects, respectively. For VO and TO, the fixed effect CG was considered. For EM, the fixed effects of CG, bull and bull breed used in *in vitro* fertilization were considered. The bull used in the IVF process as well as the breed of this bull were tested for EM, but not for TO and VO, as IVF takes place after oocyte counting. Donor's age in days (linear and quadratic components) was included as a covariate for all traits. OPU interval (linear component) was included for VO and TO.

Table 2
Descriptive statistics of the pedigree used in the analyses.

Item	Value
Total number of individuals	4,679
Total number of donors	1,641
Average inbreeding for the whole population	0.015
Average inbreeding for the donors	0.017
Percentage of individuals with known sire	88.89 %
Percentage of individuals with known dam	88.27 %
Percentage of individuals with known sire and dam	87.67 %
Percentage of donors with known sire	100 %
Percentage of donors with known dam	99.57 %
>Percentage of donors with known sire and dam	99.57 %

Table 3
Analyses of variance results (*P*-values) indicating significant effects for the number of viable oocytes (VO), the number of total oocytes (TO), and the number of embryos (EM) in the animal model.

Effects	Type of effect	*P*-values		
		VO	TO	EM
Contemporary groups	Fixed	0.000	0.000	0.000
Bull	Fixed	–[A]	–	0.000
Bull breed	Fixed	–	–	0.039
OPU interval (days)	Linear covariate	0.000	0.000	0.868
Donor's age at OPU (years)	Linear covariate	0.087	0.386	0.000
Donor's age at OPU (years)	Quadratic covariate	0.000	0.000	0.000

[A] Not included in the model for the given trait.

The animal, permanent environmental and residual effects were assumed to be random, *i.e.* $\boldsymbol{a} \sim N(0, A\sigma_a^2)$, $\boldsymbol{p} \sim N(0, I\sigma_p^2)$, $\boldsymbol{g} \sim N(0, G\sigma_g^2)$, and $\boldsymbol{e} \sim N(0, I\sigma_e^2)$, where σ_a^2, σ_p^2, σ_g^2 and σ_e^2 are the additive genetic, permanent environmental, gametic and residual variances, respectively; $\boldsymbol{A}$ is the relationship matrix, $\boldsymbol{I}$ is the identity matrix, and $\boldsymbol{G}$ is the gametic relationship matrix. ASREML software v.4.1 (Gilmour et al., 2015) was used to simultaneously estimate the variance components, and the random and fixed effects using Residual Maximum Likelihood. The ASREML output also provided Log Likelihood (LogL), Akaike Information Criterion (AIC), and Bayesian Information Criterion (BIC) values. Delta Log Likelihood values for ADm, ASm and ADSm were calculated relative to the Am model. Chi-square test statistics were obtained as twice Delta Log Likelihood values. Significance of parent-of-origin effects were verified based *p*-values for the LogL ratio test, calculated from the chi-square test statistics with the 'pchisq' function in R software (R Core Team, 2023, R version 4.2.2; R Foundation for Statistical Computing, Vienna, Austria) considering 1 degree of freedom.

3. Results

Table 4 contains the estimated variance components for TO, VO, and EM, considering animal models with or without the inclusion of parental effects. Based on AIC and BIC values, the best fit for VO was the animal model (Am). For VO, the Am model estimated an additive genetic variance of 0.13, a permanent environmental variance of 0.08, and a residual variance of 0.31. For TO, AIC values indicated the ASm model as the best fit, BIC values designed Am as the best fit. Nevertheless, ASm and ADSm model for TO had very similar LogL values. For TO, ASm estimated an additive genetic variance of 0.12, a permanent environmental variance of 0.05, and a residual variance of 0.30. For EM, Log Likelihood ratio test and AIC values defined ASm as the best fit, which estimated an additive genetic variance of 0.05, a permanent environmental variance of 0.05 and a residual variance of 0.45.

The estimated total phenotypic variance for VO ranged from 0.52 to 0.53, for TO ranged from 0.49 to 0.50, and was 0.56 for EM in all models. A significant paternal effect was found for TO. For VO and EM no parental effects were found for either parental line ($P > 0.05$). For VO and EM, maternal and paternal variances were close to zero. For TO, the paternal variance was greater than maternal variance. Also, for TO, the paternal variance represented 6 % of the total phenotypic variance in the ASm and 8 % in the ADSm.

4. Discussion

In this study, we aimed to identify parent-of-origin effects that influence the number of oocytes and embryos in Gir dairy cattle and found a significant paternal effect for the number of total oocytes. It is

Table 4
Models[A] and variance components[B] obtained from the analyses for the number of viable oocytes (VO), number of total oocytes (TO), and number of embryos (EM).

Trait	Model	LogL	χ^2	*P*-val	σ^2_p (se)	σ^2_a (se)	σ^2_{pe} (se)	σ^2_e (se)	σ^2_d (se)	σ^2_s (se)	AIC	BIC
VO	Am	−337.16	0.00	–	0.52 (0.01)	0.13 (0.02)	0.08 (0.01)	0.31 (0.00)	–	–	680.32	703.60
	ADm	−337.11	0.11	0.74	0.52 (0.01)	0.13 (0.02)	0.08 (0.01)	0.31 (0.00)	0.00 (0.01)	–	682.21	713.26
	ASm	−336.53	1.26	0.26	0.53 (0.01)	0.13 (0.02)	0.07 (0.01)	0.31 (0.00)	–	0.01 (0.01)	681.07	712.11
	ADSm	−336.53	1.26	0.26	0.53 (0.01)	0.13 (0.02)	0.07 (0.01)	0.31 (0.00)	0.00 (0.00)	0.01 (0.01)	683.07	721.87
TO	Am	53.33	0.00	–	0.49 (0.01)	0.12 (0.02)	0.07 (0.01)	0.30 (0.00)	–	–	−100.66	−77.38
	ADm	54.02	1.37	0.24	0.49 (0.01)	0.11 (0.02)	0.07 (0.01)	0.30 (0.00)	0.01 (0.01)	–	−100.04	−68.99
	ASm	55.83	5.01	0.03	0.50 (0.02)	0.12 (0.02)	0.05 (0.02)	0.30 (0.00)	–	0.03 (0.02)	−103.67	−72.63
	ADSm	55.95	5.25	0.02	0.50 (0.02)	0.10 (0.03)	0.05 (0.02)	0.30 (0.00)	0.01 (0.02)	0.04 (0.02)	−101.91	−63.10
EM	Am	−3272.37	0.00	–	0.56 (0.01)	0.06 (0.01)	0.05 (0.01)	0.45 (0.01)	–	–	6550.74	6573.99
	ADm	−3272.37	0.00	1.00	0.56 (0.01)	0.06 (0.01)	0.05 (0.01)	0.45 (0.01)	0.00 (0.00)	–	6552.74	6583.73
	ASm	−3271.19	2.36	0.12	0.56 (0.01)	0.05 (0.01)	0.05 (0.01)	0.45 (0.01)	–	0.01 (0.01)	6550.39	6581.38
	ADSm	−3271.19	2.36	0.12	0.56 (0.01)	0.05 (0.01)	0.05 (0.01)	0.45 (0.01)	0.00 (0.00)	0.01 (0.01)	6552.39	6591.12

[A] Animal model (Am); Animal + Dam gametic effect model (ADm); Animal + Sire gametic effect model (ASm); Animal + Dam gametic effect + Sire gametic effect model (ADSm).

[B] LogL: Final Log Likelihood; χ^2: Chi-square statistic test; σ^2_p: phenotypic variance; σ^2_a: additive genetic variance; σ^2_{pe}: permanent environmental variance; σ^2_e: residual variance; σ^2_d: Dam variance; σ^2_s: sire variance; se: standard error; AIC: Akaike Information Criterion; BIC: Bayesian Information Criterion.

important to reiterate that although imprinting effects are often referred to as parent-of-origin effects, they are not synonymous, that is, imprinting is an epigenetic phenomenon that alters the expression of genes according to the parental origin of their alleles, being one of possible the causes for parent-of-origin effects (Blunk et al., 2017b; Tier and Meyer, 2012).

Possible processes underlying parent-of-origin effects starts at the pre-implantation phase of embryos, where methylation imprinting can occur in differentially methylated regions of the germ cell lines. Methylation can occur, for example, by the replacement of protamines by histones in the paternal genome, active demethylation of the paternal genome and subsequent passive demethylation of both parental genomes (Li and Sasaki, 2011). Also, during embryo development towards fetal formation, the oocyte stock of mammalian females is formed, meaning that when females are born, they already carry all oocytes that will be available for use during adulthood (Seneda et al., 2021). Therefore, it is possible that the methylation imprinting process occurring during embryo development can influence the number of oocytes produced by each fetus. This might explain the significant paternal effect that we found for the number of total oocytes.

In addition, it has been reported that reproductive technology protocols may induce epigenetic changes in imprinted genes (Mangiavacchi et al., 2021). In the current study, part of the donors was produced by the use of reproductive technologies, such as *in vitro* fertilization. Mangiavacchi et al. (2021) mention that embryos generated by assisted reproduction technologies may show morphological abnormalities at different stages of embryonic development as well as in the postnatal period associated with hypergrowth, which can indicate epigenetic failures. This suggests that specific epigenetic events may have occurred during donors' formation, and we speculate that this may have affected their oocytes production.

It is known that during mouse embryo development, imprints are acquired in a sex-specific manner in the mature germline, with the establishment of paternal imprints occurring prenatally and maternal imprints occurring postnatally (Plasschaert and Bartolomei, 2014). The zygote receives the paternal and maternal epigenetic imprints that were formed in the germline through fertilization, and these imprints are preserved throughout growth and adulthood (Li and Sasaki, 2011). In cattle, DNA-methylated regions identified in the paternal germline were related to the fertility of bulls and their daughters (Costes et al., 2022; Zhang et al., 2023a, 2023b). DNA methylation patterns from bulls used in artificial insemination were found in genomic regions covering genes related to spermatogenesis and early embryonic development (Costes et al., 2022; Štiavnická et al., 2022). Zhang et al. (2023a) found that most of the methylated regions in bovine sperm samples were distributed on the X and Y chromosomes, demonstrating that the sex chromosomes play essential roles in bull fertility. In another study, Zhang et al. (2023b) selected 12 bulls classified with high or low daughter fertility to study their enzymatic methylation and found methylation profiles in sperm samples distributed more on the X chromosome than on the autosome, associated with daughter fertility. The daughter fertility index studied by Zhang et al. (2023b) is a combination of reproductive traits, such as age at first service, the 56-day non-return rate for heifers/cows, the interval from calving to the first service, and the interval from insemination to conception (heifer/cow). This indicates that paternal epigenetic effects are associated with daughter fertility.

Nevertheless, regarding imprinting genes and parent-of-origin effects reported for cattle, only one work was found for parent-of-origin effect in the Catalogue of Parent of Origin Effects (Morison et al., 2005, www.otago.ac.nz/IGC), which is related to milk production (Kuehn et al., 2007). This demonstrates the need for more studies exploring imprinting and parent-of-origin effects in bovine and other species. In the current study, parent-of-origin effects for the number of total oocytes, viable oocytes and embryos in dairy Gir cattle were explored using a gametic relationship approach (Tier and Meyer, 2012). In our previous work (Rocha et al., 2022), we had the same population data sample, but used repeatability and random regression models on BLUPF90 family programs (Misztal et al., 2002). The difference from our previous study to this one is the addition of parental gametic effects, where parent-of-origin effects can be identified, which is not possible using only the animal model. The identification of a parental effect can influence the selection of animals, that is, the focus can be given to the sire or the dam at the time of selection for a given trait. In the current study, ASREML software (Gilmour et al., 2015) was used since it was easier to include the gametic relationship matrices.

Despite the use of different programs, variance components were similar between studies. The additive genetic variance found by Rocha et al. (2022) using BLUPF90 family programs was 0.13 for VO, 0.12 for TO and 0.06 for EM. In the current work, using ASREML software, the additive genetic variance was 0.13 for VO regardless the model, it ranged from 0.10 to 0.12 for TO among models and it was 0.05 or 0.06 for EM. The permanent environmental variance found by Rocha et al. (2022) for VO was 0.08 and in this work it was 0.07 or 0.08 depending on the model. For TO, Rocha et al. (2022) found a permanent environmental variance of 0.07 and in this work it was 0.05 or 0.07. For EM, the permanent environmental variance found was 0.05 in both studies. Values of residual variance were 0.31 for VO, 0.30 for TO and 0.45 for EM in both studies. The existence of genetic variation for oocytes and embryos allow for selection for these traits in the Gir breed. Also, greater

values of residual variance than additive genetic variance were expected considering that the data came from five farms and different Ovum Pick Up/*in vitro* fertilization processes were used.

Regarding the parent-of-origin variances, most parent-of-origin studies were performed for meat and carcass traits in pigs (de Vries et al., 1994; Neugebauer et al., 2010a) and cattle (Blunk et al., 2017a, 2017c, 2017b; Engellandt and Tier, 2002; Inoue et al., 2021; Neugebauer et al., 2010b; Okamoto et al., 2019; Tier and Meyer, 2012). In addition to production traits, Amiri Roudbar et al. (2018) applied the gametic relationship matrix approach to study reproduction traits in sheep and found maternal imprinting effects for total litter weight at weaning per ewe lambing. Tier and Meyer (2012) mention that most models applied for genomic selection consider additive genetic effect with an equal contribution from both parents, which undervalue loci modified by their parents for heterozygous offspring and could lead to an inefficient selection.

To the best of our knowledge, there are currently no other parent-of-origin studies for oocyte and embryo related-traits in cattle. Although the number of oocytes and embryos are not yet included in genetic evaluations of the Dairy Gir National Breeding Program, Gir cattle producers collect this information from Gir donors in order to assess the reproductive quality of the herd and increase oocyte and embryo productivity. The present study identifies the existence of parent-of-origin effects on the number of oocytes and embryos, which has never been explored in the Gir breed. The results of this work may help to reinforce the existence of imprinting effects on traits of economic impact in livestock farming, since these effects are little explored in animal breeding programs. These results may also contribute to future research to verify the expression of parental alleles on the production of oocytes. Furthermore, this study opens the possibility of including them in breeding programs due to their economic impact. It is worth noting that our study is a first step to identify the presence or absence of parent-of-origin effects on the number of oocytes and embryos. Future studies using molecular approaches might contribute with new insights; for example, identifying imprinted genomic regions from each parental line.

5. Conclusion

We found a paternal effect for the number of total oocytes in Gir cattle. The paternal effect explained 6 % of the total phenotypic variance. Considering the importance of reproductive traits for livestock production and taking into account that we found a paternal effect for the number of total oocytes emphasizes the need for studies to evaluate the parent-of-origin effects of alleles for reproductive traits in cattle. Furthermore, statistical models considering only additive effects may underestimate parental genomic imprinting modifications from the animals under genetic evaluation.

CRediT authorship contribution statement

Renata de Fátima Bretanha Rocha: Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Arielly Oliveira Garcia:** Investigation, Visualization. **Mateus Guimarães dos Santos:** Investigation, Visualization. **Pamela Itajara Otto:** Investigation, Methodology, Visualization. **Marcos Vinícius Barbosa da Silva:** Data curation, Resources, Visualization. **Marta Fonseca Martins:** Data curation, Resources, Visualization. **Marco Antônio Machado:** Data curation, Resources, Visualization. **João Claudio do Carmo Panetto:** Data curation, Resources, Visualization, Conceptualization. **Mario P.L. Calus:** Formal analysis, Investigation, Methodology, Software, Validation. **Jeremie Vandenplas:** Formal analysis, Investigation, Methodology, Software, Validation. **Simone Eliza Facioni Guimarães:** Conceptualization, Investigation, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

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