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Energy balance influences number of ovulations rather than embryo quality in the pig

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ABSTRACT

The present study was undertaken to examine the effect of feed restriction on ovulation rate and *in vivo* blastocyst development in gilts and sows. In the first experiment, gilts were feed restricted (1 vs. 2.5 times maintenance requirement) during the luteal and follicular phases before ovulation. In the second experiment, primiparous sows were feed restricted (ad lib vs. 60% thereof) during the last week of lactation before weaning. Gilts and sows were slaughtered at 5 days after ovulation to determine ovulation rate and blastocyst development. Blastocysts were also differentially stained to determine the effect of feed restriction on total, trophectoderm, and inner cell mass cell numbers. In both experiments, feed restriction delayed ovulation and reduced the number of ovulations in gilts (14.8 ± 1.3 vs. 12.0 ± 0.2; $P < 0.05$) and in sows (19.9 ± 1.0 vs. 18.4 ± 0.7). The number of blastocysts recovered on Day 5 was similarly reduced in gilts (12.0 ± 1.7 vs. 9.1 ± 1.1; $P < 0.10$) and in sows (15.9 ± 1.5 vs. 14.7 ± 1.0). However, feed restriction did not affect total, trophectoderm, or inner cell mass cell numbers in gilts or sows. In conclusion, the present study reported that energy balance influences ovulation rate and blastocyst number rather than blastocyst viability as measured by cell number.

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1. Introduction

Feed intake in primiparous lactating sows is generally insufficient to meet nutrient requirements for milk production, resulting in excessive mobilization of body reserves [1,2]. Effects of metabolic state on reproduction have been investigated in restrict-fed sow models; with effects on ovulation rate, embryo survival, or both being reported [3–7]. Severe catabolism in lactating primiparous sows influences ovarian activity by reducing postweaning LH secretion [8,9], causing delays in ovarian follicle maturation and longer weaning-to-estrus intervals [10]. Preweaning LH secretion is also reduced in sows that are highly catabolic [2,3] suggesting follicle development may already be affected before weaning, with carry-over effects after weaning.

Baidoo et al. [11] reported that even if sows are fed ad libitum after weaning, feed restriction during the preceding lactation still impacts on embryo survival. Similarly, feed restriction in cyclic gilts during the luteal phase preceding the follicular phase reduces the number of antral follicles [12], ovulation rate, and embryo number [13]. It has been suggested that a catabolic state affects follicular growth and oocyte maturation, compromising the number of preovulatory follicles that develop after weaning [14,15]. In mice, nutrition can influence the number of inner cell mass (ICM) cells in blastocysts which in turn can influence implantation rate [16]. Whether a similar relationship exists in pigs, has not been reported. However, this may explain the relatively high early embryonic loss seen in this species.

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The aim of the present study therefore was to determine if feed restriction in gilts and sows influences *in vivo* embryo development, in particular blastocyst viability as measured by ICM number.

2. Material and methods

The study was approved by the University of Adelaide's Animal Ethics Committee (M-2012–83). In experiment one, prepubertal gilts weighing 107 ± 2.4 kg were induced to cycle with 400 IU of pregnant mare's serum gonadotrophin and 200 IU of human chorionic gonadotrophin (PG 600; Intervet Pty Ltd., Bendigo East, Vic., Australia) at 24 weeks of age. Prepubertal status was diagnosed using transcutaneous ultrasound to confirm absence of corpora lutea and any preovulatory follicles before injection. Fence line boar exposure in a detection-mating-area was used once per day to detect estrus. Gilts that found estrus within 1 week (n = 41) were individually housed and fed a standard gilt developer diet (13.2 MJ DE/kg; 150 g/kg crude protein), at maintenance (restricted) or at 2.5 times maintenance (control) from 5 days after puberty until their second ovulation (approximately 16 days). Maintenance was calculated as body weight $(BW)^{0.75} \times 0.46$-MJ digestible energy per day (BW in kg). After the first luteal phase, gilts were injected with two injections of 500-mg intramscular cloprostenol at 12-hour intervals (Juramate; Jurox Pty Ltd., Rutherford, Vic., Australia) 12 days after their first ovulation, to synchronize the start of the (second) follicular phase and time of ovulation was monitored by ultrasound every 12 hours (Aquila Pro Vet. Esaote Europe B.V., Maastricht, The Netherlands).

Boar exposure was resumed the day after cloprostenol injection to detect estrus. Gilts were inseminated every day of estrus with pooled semen containing 3 billion sperm, until ovulation was determined (on average two inseminations). Animals were then slaughtered at a local abattoir at 5 days (4.25–5.25 days) after ovulation and the reproductive tracts collected. Embryos were recovered by flushing the whole reproductive tract with PBS and recovering these under low magnification. Ovulation rate, number of embryos, and the number of these that were blastocysts and the stage of blastocyst development (early, expanded, and hatched) were recorded. Blastocysts were differentially stained to determine blastocyst, trophectoderm, ICM, and total cell number. Blastocysts were differentially stained using a modified method as previously described [17]. Zonae pelucidae of blastocysts were removed by incubating in 0.5% pronase in Dulbecco's PBS. They were then washed in modified Eagle's media (MEM) containing Hepes and 0.8% (w/v) polyvinylpyrrolidone (PVP). Trophectoderm cells were lysed by incubating zona-free blastocysts on ice for 30 minutes in Hepes-MEM-PVP containing 10-mM trinitrobenzenosulfonic acid (pH 8.5), washing in Hepes-MEM-PVP, and then incubating at 37 °C for 30 minutes in a 1:10 dilution of antidinitrophenol bovine serum albumine in Hepes-MEM-PVP. Blastocysts were then washed in Hepes-MEM-PVP and incubated at 37 °C for 30 minutes in a 1:5 dilution of guinea pig complement serum in Hepes-MEM-PVP. The trophectoderm and ICM cells were then stained with 0.01-mg/mL propidium iodide and 0.05-mM bisbenzimide (Hoechst 33258), respectively. For cell counting, blastocysts were fixed in ethanol at 4 °C, mounted in glycerol on microscope slides, and examined using a fluorescence microscope (Diaphot-TMD; Nikon Corporation, Tokyo, Japan) fitted with a UV-2A filter combination having a 330–380-nm excitation filter and a 420-nm barrier filter. Trophectoderm cells fluoresced red, whereas ICM cells fluoresced blue. The remaining embryos were frozen to determine gene expression in the advent that a difference in cell number was reported.

In experiment two, 34 lactating, primiparous sows were housed individually in farrowing crates, and fed an increasing amount of a lactation diet (14.1-MJ DE/kg; 169-g/kg crude protein) until they reached ad libitum feed intake at about 10 days after farrowing. Litter size was standardized to 11 piglets at the start of lactation. Sows were fed ad libitum until allocation to treatments at 1 week before weaning (Day 24 of lactation). Treatments were either ad libitum feeding (control, n = 15), or pair feeding at 60% of the intake of the paired counterpart (restricted, n = 15) the latter which was determined on a daily basis, for the remainder of lactation. Pairs were on the basis of intake before allocation. The average feed intake in the last week of lactation was 6.7 kg for ad lib sows and 4.2 kg/day for restrict-fed sows. Sows with a feed intake lower than 4.5 kg before allocation were excluded from the trial. Sows and their litters were weighed at the start of lactation, 1 day before allocation to treatments, and at weaning. Feed intake of the sows was determined on a daily basis. These measurements were used to calculate energy balance (MJ ME/day) based on energy intake (feed intake) and energy requirements based on BW of the sow and weight gain of the litter (g/day): energy balance $= (0.46 \times [BW^{0.75}]) + (0.02859 \times$ weight gain of the litter$) - (0.52 \times LS)$, with LS = litter size. This estimation was based on Noblet et al. [18].

After weaning, sows in control and restricted treatments were treated the same in terms of feeding (3 kg per day of a standard dry sow diet), boar exposure, heat detection, and insemination. Heat detection, insemination, and ultrasound were similar to the procedure described previously for experiment one. Embryos were recovered at Day 5 (4.75–5.25 days) after ovulation by flushing tracts and recovering these under low magnification. Ovulation rate, number of embryos, and the number of these that were blastocysts were recorded. Approximately half of these were differentially stained to determine, total cell number, trophectoderm, and ICM cell number as in experiment one. The remaining embryos were frozen to determine gene expression in the advent that difference in cell number was reported.

Statistical analyses were performed using SAS [19]. Continuous variables such as BW were analyzed for treatment effects using ANOVA, assuming normal distribution of variables. Embryo cell numbers were normally distributed but nevertheless were also analyzed after a 2-log transformation, which yielded the same outcomes as with untransformed data, and therefore the results are not presented. For analysis of embryo cell number, age at slaughter was also included as a covariate. Binomial variable such as heat expression were analyzed using a chi-square.

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