Consequences of different patterns of feed intake during the estrous cycle in gilts on subsequent fertility

F. R. Almeida, R. N. Kirkwood, F. X. Aherne and G. R. Foxcroft

J Anim Sci 2000. 78:1556-1563.

Consequences of different patterns of feed intake during the estrous cycle in gilts on subsequent fertility[1,2]

F. R. C. L. Almeida[3], R. N. Kirkwood[4], F. X. Aherne[5], and G. R. Foxcroft[6]

Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, AB, Canada T6G 2P5

ABSTRACT: The impact of different patterns of feed restriction between d 1 and 15 of the estrous cycle on subsequent reproductive performance of 23 trios of littermate gilts was tested. Some gilts were fed a high plane of nutrition (HH gilts) throughout the cycle, in contrast to HR gilts, which were restricted from d 8 to 15, and RH gilts, which were restricted from d 1 to 7. During feed restriction, weight gain in RH gilts (2.5 ± .7 kg) was lower (P = .006) between d 1 and d 7 than in their HH and HR littermates (5.6 ± .7 and 5.6 ± .8 kg, respectively) and it was lower (P = .0001) in HR gilts (5.5 ± .5 kg) between d 8 to d 15 than in their HH and RH counterparts (8.5 ± .4 and 9.4 ± .5 kg, respectively). There were no differences in backfat changes among groups. Embryonic survival in HR gilts at d 28 of gestation (68.3 ± 4.8%) was lower (P < .05) than in HH and RH gilts (83.6 ± 4.3 and 81.7 ± 4.5%, respectively). Plasma progesterone concentrations in HR gilts were lower (P < .05) at 48 and 72 h after onset of standing estrus (.82 ± .2 and 3.6 ± .5 ng/mL, respectively) than in HH and RH gilts (1.44 ± .2 and 1.24 ± .2 ng/mL, 5.0 ± .4 and 5.0 ± .5 ng/mL, respectively at 48 and 72 h). No differences in ovulation rate were observed among treatments. Placental area was positively correlated to embryo size at d 28 (embryo size = .0003 × (area) + 18.35; r = .28, P = .03) but placental volume was negatively correlated to the number of embryos in utero (placental volume = –4.317 × (number) + 207.55, r = –.39, P = .002). These data demonstrate that the timing of feed restriction during follicular development has important consequences for subsequent embryo survival, possibly mediated by differences in progesterone concentrations in early pregnancy.

Key Words: Embryos, Gilts, Nutrition, Progesterone, Reproduction

 J. Anim. Sci. 2000. 78:1556–1563

Introduction

Reproductive efficiency is an important goal in the swine industry and is represented by the number of pigs weaned per sow per year (Foxcroft et al., 1995). Replacement gilts are a critical component of the breeding herd and it is essential to improve fertility in these animals, emphasizing genetics, nutrition, and management practices.

Several studies have demonstrated the interactions between nutrition and reproduction in gilts (Armstrong and Britt, 1987; Cox et al., 1987; Booth et al., 1994) and lactating sows (Koketsu et al., 1994; Zak et al., 1997a). In cyclic gilts, a positive relationship exists between feed intake and ovulation rate (Flowers et al., 1989; Beltranena et al., 1991), and nutritional effects on ovulation rate seem to be insulin-dependent (see Cox, 1997). Even short periods of feed restriction in the prepubertal gilt produce inhibitory effects on ovarian development (Cosgrove et al., 1992; Booth et al., 1994). However, the effects of different patterns of feeding during the 19-d period of pre-ovulatory follicular development predicted by Morbeck et al. (1992) on subsequent fertility are still unclear.

In recent studies in primiparous sows (Zak et al., 1997a), nutritional changes were used to create different patterns of catabolism during a lactation period of 28 d and differentially affected reproductive performance. Low ovulation rates and marginally extended

[1]This research was financially supported by the Alberta Agric. Res. Inst., the Alberta Pork Producers Development Corp., and the Natural Sciences and Engineering Res. Council.

[2]The authors gratefully acknowledge the Swine Research Unit staff members and Shirley Shostak, Susan Novak, and Jiude Mao for their help, Pig Improvement (Canada) Ltd for provision of experimental animals, and Alberta Swine Genetics Corp., for the semen.

[3]F. Almeida was supported by a scholarship from CAPES (Brazil).

[4]Present address: Royal Veterinary College, University of London, U.K.

[5]Present address: Alberta Agriculture, Food and Rural Development, Swine Research Group, O. S. Longman Building, 6909-116 St. Edmonton, AB, Canada T6H 4P2.

[6]Correspondence: phone: (780) 492-7661; fax: (780) 492-9130; E-mail: gfoxcroft@afns.ualberta.ca.

Received July 7, 1999.

Accepted December 3, 1999.

weaning-to-estrus intervals were observed in response to any pattern of feed restriction compared to sows fed to appetite throughout lactation. However, decreased embryo survival to d 28 was only observed in sows subjected to restriction in late lactation.

The aim of the present experiment was to develop a comparable gilt model to further test the hypothesis that different metabolic states, achieved by different patterns of feed restriction at critical times before recruitment of follicles into the pre-ovulatory hierarchy, differentially affect the reproductive performance of gilts.

Materials and Methods

Pretreatment of Gilts

The first target of the study was to have groups of growth-matched, littermate gilts with an age of 160 d and weighing approximately 90 kg when first stimulated with vasectomized boars. To achieve this target, prospective littermates were identified at weaning and were given ad libitum access to a series of three diets: a weaner diet until approximately 25 kg body weight, a grower diet until approximately 60 kg body weight, and, finally, a gestation, rather than a finisher, diet to limit their growth rate until approximately 90 kg body weight (Table 1). Throughout this period, gilts that had very high or very low body weights compared to their littermates were taken out of the study to create littermate groups with similar prepubertal growth rates. Any lame gilts were also culled from the experiment.

Gilts that remained in the study were directly exposed to vasectomized boars for at least 15 min daily from 160 d of age (six gilts:one boar) until the last gilt had displayed pubertal estrus. At this stage, gilts were weighed, backfat thickness at P_2 was measured (Renco Lean-Meter, Renco, Minneapolis, MN) and individually fed a grower diet twice daily at a level to meet their metabolic requirements and to achieve a growth rate of 750 g/d, which was considered to be achievable using the diet fed, the genetic potential of the gilts, and expected voluntary feed intake.

Digestible energy (DE) requirements for maintenance were calculated as metabolic body weight ($BW^{.75}$) $\times$ 110 kcal (NRC, 1998), and the energy requirements for growth, based on the assumption that tissue accretion comprises 77% lean and 22% fat (C. de Lange, 1997, personal communication), was estimated as 4 Mcal. On the basis of these calculations, the energy requirement for maintenance, plus 4 Mcal, divided by the energy content of the diet (grower diet = 3,314 kcal DE), gave the amount of feed intake per day. Gilts were weighed weekly (without restrictions of feed or water), and their feed intakes were adjusted within a 10-kg range of body weight, equivalent to feed increments of 100 g.

To synchronize second estrus of the females within a littermate group, from d 15 of their first estrous cycle each gilt received the oral progestagen altrenogest (Regu-Mate, Hoechst-Roussel Vet., Canada) until the last littermate in estrus received at least 5 d of Regu-Mate treatment. After the withdrawal of Regu-Mate, gilts were fed to appetite twice daily (0700 and 1400), and daily feed weighbacks were carried out to estimate "unrestricted" feed intake at this stage. Gilts were tested for estrus twice a day (0700 and 1900 h) with mature, vasectomized boars until the onset of second estrus. All gilts came into estrus within 6 d after Regu-Mate withdrawal, with a mean interval of 26 d between first and second estrus. Infertile breedings were allowed at second estrus as the best way to confirm standing estrus, and to maintain good libido in the vasectomized boars.

Table 1. Dietary composition, as formulated, of weaner, grower, and gestation diets used in the experiment

Item	Weaner	Grower	Gestation
Ingredient, %			
Wheat	26.8	—	—
Barley	9.8	75.9	86.0
Soybean meal	15.8	12.0	4.0
Canola meal	—	6.1	4.5
Oat groat	19.5	—	—
Fish meal	4.2	—	—
Lysine	.2	.2	—
Whey	15.6	—	—
Limestone	1.0	1.1	1.6
Dicalcium phosphate	1.2	.9	1.4
Salt	.5	.4	.5
Oil	4.3	2.3	1.0
Premix[a]	1.1	1.1	1.0
Nutrients			
Digestible energy, kcal/kg	3,544	3,314	3,120
Crude protein, %	20.15	17.30	13.75
Calcium, %	.86	.72	.93
Total phosphorus, %	.75	.66	.70
Lysine, %	1.30	.99	.56
Methionine + cystine	.66	.55	.44
Threonine, %	.76	.61	.47

[a]Premix composition per kilogram of diet: weaner and gestation diets: vitamin A, 10,000 IU; vitamin D, 1,000 IU; vitamin E, 80 IU; vitamin K, 2 mg; vitamin B_{12}, 30 μg; riboflavin, 12 mg; niacin, 40 mg; pantothenic acid, 25 mg; choline, 1,000 mg; biotin, 250 μg; folic acid, 1,600 μg; ethoxyquin, 5 mg; Fe, 150 mg; Mn, 12 mg; Zn, 120 mg; Cu, 20 mg; I, 200 μg; Se, 300 μg. Grower diet: vitamin A, 5,000 IU; vitamin D, 500 IU; vitamin E, 40 IU; vitamin K, 2 mg; vitamin B_{12}, 30 μg; riboflavin, 12 mg; niacin, 40 mg; pantothenic acid, 25 mg; choline, 300 mg; biotin, 150 μg; ethoxyquin, 5.0 mg; Fe, 150 mg; Mn, 12 mg; Zn, 100 mg; Cu, 20 mg; I, 200 μg; Se, 300 μg.

Experimental Treatments

All experimental procedures were carried out in accordance with the guidelines of the Canadian Council for Animal Care and under authorization from the University Animal Policy and Welfare Committee.

After the withdrawal of Regu-Mate, littermate gilts were randomly allocated to one of three feeding regimens. A positive control group (**HH**) was fed a high plane of nutrition, some gilts were feed-restricted from

d 8 to 15 (**HR**), and others were feed-restricted from d 1 to 7 (**RH**). If it was not possible to allocate three littermates, pairs of gilts were randomly allocated to the two main treatments (HR, RH) and matched with a non-littermate HH gilt according to body weight and age at puberty. Of a total of 23 groups, 7 were matched with a non-littermate gilt.

To match the duration of feed restriction to the same 7-d periods used in previous lactating sow studies (Zak et al., 1997a) but still allow a period of unrestricted feeding in all treatment groups during the final phase of follicular growth (equivalent to the weaning-to-estrus period in the sow), different patterns of feed allowance were imposed between d 1 and 7 (early luteal phase) and d 8 and 15 (late luteal phase) of the cycle; all gilts were then fed at the same high rate of intake between d 16 and estrus (follicular phase). All feed allowances were equally divided between two meals fed at 0700 and 1400.

Defining d 0 as the 1st d of the second standing heat, the HH, HR and RH treatments were applied as follows:

Group HH. Energy feed intake was set at 95% of "unrestricted" energy intakes established during the period of feeding from d 16 and onset of second standing estrus. This was equivalent to an energy intake of 2.8 × maintenance and was fed to HH gilts from d 1 to 7 and d 8 to 15 of the cycle based on metabolic body weights at d 0 and 7, respectively. This energy allowance ensured that 1) all gilts would consume their allotted feed and 2) the restriction in energy intake relative to "unrestricted" feeding was proportional to the energy deficit seen in the unrestricted first-parity sows in late lactation in the study of Zak et al. (1997a).

Group RH. From d 1 to 7 the energy allowance of these gilts was set 25% below that of the HH group (i.e., 2.1 × maintenance). This level of energy restriction was considered to be proportionally the same as that imposed in sows restricted during the last week of lactation, compared to unrestricted sows in the study of Zak et al. (1997a). From d 8 to 15, RH gilts were fed as HH gilts, at 2.8 × maintenance based on metabolic body weights at d 7.

Group HR. Pigs in this group were fed the same as HH gilts from d 1 to 7, and then at 2.1 × maintenance from d 8 to 15, based on metabolic body weights at d 7.

From d 16 until breeding during their third standing estrus, all gilts received 2.8 × maintenance allowances based on d-15 metabolic body weights. Backfat was measured in all animals at d 0, 7, and 15 and at the onset of estrus. Gilts were checked for estrus using the back-pressure test during periods of fenceline contact with mature boars twice daily (0700 and 1900) and were artificially inseminated 12 and 24 h after the first observed standing estrus with pooled semen (3×10^9 spermatozoa/dose) from the same group of boars (Alberta Swine Genetics, Leduc, AB, Canada) specifically designated for this experiment. Immediately after first mating, all gilts received 1.5 × maintenance requirements (2.05 ± .11 kg) until slaughter at d 28 of pregnancy. The diets were nutritionally balanced in terms of amino acids, vitamins, and minerals to meet NRC (1988) recommended nutritional requirements.

All gilts were slaughtered at a local abattoir on d 28 ± 3 of pregnancy. Reproductive tracts were recovered and ovulation rate was estimated by counting the number of corpora lutea on each ovary. To collect data on placental and embryonic development, the wall of the uterine horns was cut longitudinally along the antimesometrial side, starting at the utero-cervical junction. Before removing any embryos from the uterus, allantoic fluid volume was determined by draining this fluid into measuring cylinders. The length and width of the allantochorionic placenta, excluding the necrotic tips of the chorion, were measured in utero under minimal stretch and used to calculate placental area. The number of live embryos and crown–rump length (size) of each embryo were recorded. To provide an objective measure of abnormal development, embryos were classified as being nonviable on the basis of a crown–rump length significantly less than the mean for all embryos recovered from that gilt (Jindal et al., 1996). Embryo survival was expressed as the percentage of corpora lutea represented by live embryos recovered. To determine whether the previous feeding regimen had subsequent effects on the pattern of circulating progesterone in early pregnancy, a series of blood samples were taken by acute venipuncture 36, 48, 72, and 96 h after the onset of estrus and plasma progesterone concentrations determined using an established radioimmunoassay (Coat-a-Count Progesterone, Diagnostic Products, Los Angeles, CA) previously validated for use with porcine plasma without extraction (Mao and Foxcroft, 1998). The sensitivity of the assay, defined as 88% of total binding, was .01 ng/tube. The intra- and interassay CV were 8.0 and 18.5%, respectively.

Statistics

The data were analyzed as a randomized complete block design, with three treatments in 23 blocks, each block consisting of a group of three littermates. Treatment effects on ovulation rate, embryonic survival, body weight, and backfat changes to estrus onset were analyzed using the general linear model (GLM) procedure of SAS (1990). Embryonic survival data were arcsine-transformed before analysis. The analysis of body weight and backfat changes to estrus onset included the effects of block and treatment in the model with body weight and backfat at d 0 as covariates. Because it was not possible to slaughter all gilts exactly at d 28 of pregnancy, correlation analyses were performed using residuals of embryo size, placental area, allantoic fluid volume, and embryo number. All these measurements were based on averages per gilt and were corrected for block, treatment, day, and day × treatment interaction. Because progesterone concentra-

tions did not present a normal distribution, the data were log-transformed prior to analysis and were analyzed by repeated measures analysis of variance, using the repeated measures GLM procedure of SAS (1990). The complete model included treatment, block, and time as the main effects, gilt was the experimental unit, and gilt within treatment × block interaction was used as the error term. In the event that significant treatment effects were established, multiple comparisons were performed using probability of differences (pdiff) between least squares means, adjusted by Tukey-Kramer (SAS, 1990).

Results

Animals

Of the 69 gilts initially allocated to treatment, 8 were excluded from the experiment. In the HH group, one gilt had a prolonged estrous cycle (> 24 d). In the HR group, one gilt had a polycystic ovary at slaughter, and three other gilts did not present a well-defined standing estrus and were not pregnant at d 28. In the RH group, one gilt had a broken leg and two others had prolonged estrous cycles.

Body Weight and Backfat Changes

Feed intake, body weight and weight change, backfat thickness at P_2, and backfat change of gilts are summarized in Table 2.

The RH gilts had a lower growth rate (P = .0056) during the period of feed restriction (d 1 to d 7) than both the HR and HH groups. The HR group also had a lower growth rate (P = .0001) during the period of feed restriction (d 8 to d 15) than its HH and RH counterparts. There was no difference (P > .05) in growth rate among groups from d 16 until onset of estrus, probably due to their low feed intake in this period. Backfat changes were not different among groups during the experimental period. However, backfat measurements were greater in HH gilts on d 15 (P = .0445) and at estrus (P = .02) than in RH gilts; backfat in HR gilts was intermediate.

Embryonic Survival Rate

Although ovulation rate and number and size of embryos in utero were not affected by treatment, embryonic survival was lower (P = .038) in HR gilts than in HH and RH gilts (Table 3). A significant litter effect was observed for ovulation rate among gilts (P = .03).

Progesterone Concentrations

Plasma concentrations of progesterone in early pregnancy were affected by previous nutritional treatment (P < .05). Progesterone concentrations in all treatment groups increased with time (Figure 1). However, this increase occurred later in HR than in HH and RH gilts, with a difference in plasma concentrations evident at 48 (.8 ± .2 vs 1.4 ± .2 and 1.2 ± .2 ng/mL in HH and RH, respectively; P = .009) and 72 h (3.6 ± .5 vs 4.9 ± .4 and 5 ± .5 ng/mL in HH and RH, respectively; P = .049).

Table 2. Feed intake, body weight, body weight change, backfat thickness, and backfat change of HH, HR, and RH gilts at d 0, 7, and 15 and at estrus (least squares means ± SEM)

Item	HH	HR	RH
Feed intake, kg[a]			
d 1 to 7	3.0 ± .1	2.9 ± .1	2.2 ± .1
d 8 to 15	3.5 ± .1	2.7 ± .1	3.4 ± .1
d 16 to Estrus	3.0 ± .1	3.0 ± .1	2.8 ± .1
Body weight, kg			
d 0	133.0 ± 2.1	132.0 ± 2.3	129.8 ± 2.1
d 7	137.0 ± .7[b]	136.8 ± .8[b]	133.7 ± .7[c]
d 15	145.4 ± .6[d]	142.3 ± .6[e]	143.0 ± .6[c]
Estrus	146.2 ± .9	144.7 ± 1.0	143.7 ± .9
Body weight change, kg			
d 1 to 7	5.6 ± .7[f]	5.6 ± .8[f]	2.5 ± .7[g]
d 8 to 15	8.5 ± .4[h]	5.5 ± .5[i]	9.4 ± .5[h]
d 16 to Estrus	.9 ± .7	2.4 ± .7	.6 ± .7
Backfat, mm			
d 0	12.8 ± .4	12.0 ± .4	12.2 ± .4
d 7	13.0 ± .2	13.1 ± .3	12.5 ± .2
d 15	14.1 ± .2[x]	13.6 ± .2[xy]	13.2 ± .2[y]
Estrus	14.2 ± .2[w]	13.5 ± .3[wz]	13.1 ± .2[z]
Backfat change, mm			
d 1 to d 7	.6 ± .2	.8 ± .3	.2 ± .2
d 8 to d 15	1.0 ± .3	.4 ± .3	.7 ± .3
d 16 to Estrus	.1 ± .2	−.02 ± .2	−.1 ± .2

[a]Feed offered (kg): d 1 to d 7, 3.5 ± .04, 3.5 ± .04, 2.6 ±.04; d 8 to 15, 3.6 ± .04, 2.7 ± .06, 3.6 ± .04; d 16 to estrus, 3.8 ± .04, 3.8 ± .04, 3.8 ± .04, respectively, for HH, HR, and RH gilts.

[b,c,d,e,f,g,h,i,w,x,y,z]Least squares means within rows with different superscripts differ (P<.05).

Embryo-Placental Associations

Placental area and volume were not affected by previous nutritional treatments (P > .05) but were affected by litter of origin (P = .009 and P = .003, respectively).

Notwithstanding this litter effect, allantoic fluid volume and area of the allantochorionic membranes were correlated (volume = .0073 × (area) + 37.6, r = .35, P = .005). Placental area was also positively correlated

Table 3. Reproductive characteristics at d 28 of gestation in gilts subjected to different feed regimens before mating (least squares means ± SEM)

Treatment (n)	Ovulation rate	No. of live embryos	Embryo size, mm	Embryo survival, %
HH (22)	17.1 ± .6	14.3 ± .9	22.5 ± .5	83.6 ± 4.3[a]
HR (19)	18.5 ± .6	12.8 ± 1.0	21.7 ± .5	68.3 ± 4.8[b]
RH (21)	17.7 ± .6	14.7 ± 1.0	23.0 ± .5	81.7 ± 4.5[a]

[a,b] Least squares means within columns with different superscripts differ, P = .038 (analysis based on arcsine-transformed data).

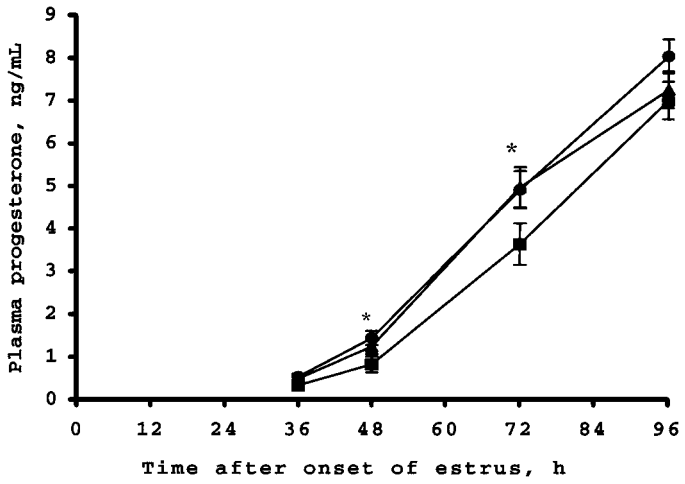

Figure 1. Plasma progesterone concentrations (least squares means ± SEM) of gilts at 36, 48, 72, and 96 h after onset of estrus (●, HH; ■, HR; ▲, RH). *Values differ ($P < .05$).

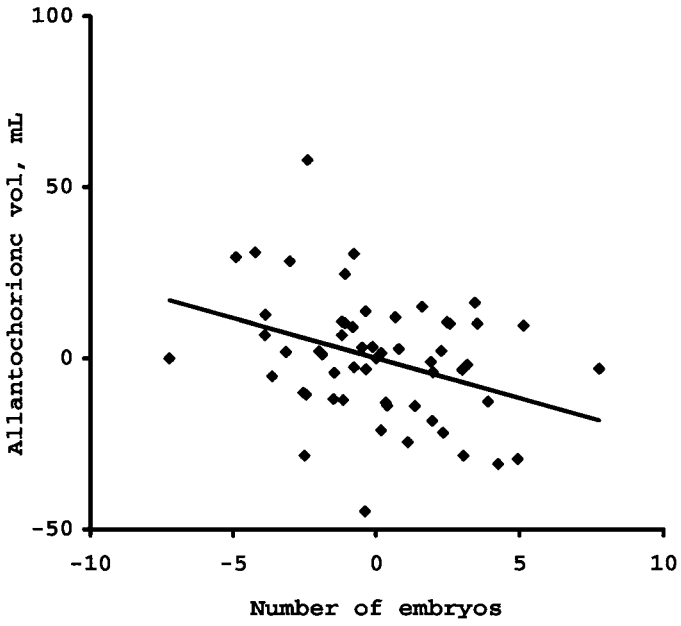

Figure 3. Relationship between residual allantochorionic volume (y-axis) and residual number of embryos (x-axis) after correction for block, treatment, and day. Allantochorionic volume and number of embryos are negatively correlated (plot of residuals: placental volume = –4.317 × (number) + 207.55, r = –.39, $P = .002$).

to embryo size at d 28 (embryo size = .0003 × (area) + 18.35, r = .28, $P = .03$; Figure 2), and placental volume was negatively correlated to the number of embryos in utero (placental volume = –4.317 × (number) + 207.55, r = –.39, $P = .002$; Figure 3).

Discussion

Food availability is certainly the most important environmental factor that can affect growth. This was suggested by Williams et al. (1974) in a study in which rats were allowed to grow normally until a particular stage of development, and further growth was then inhibited by restricting the amount of food available to them. Bikker et al. (1996) also demonstrated in finishing gilts that realimentation after a period of feed restriction resulted in compensatory gain and increased feed efficiency. Furthermore, Booth et al. (1994) reported that gut fill clearly played a role in live weight variation and made a greater contribution to live weight in gilts fed to appetite. Therefore, the lower growth rate of HR and RH gilts when subjected to feed restriction and a trend toward compensatory growth after realimentation was expected. The lack of an effect on backfat change is likely due to the modest level of feed restriction used (2.1 × maintenance), which allowed the animals to continue growing, though at a slower rate than their counterparts on a high plane of nutrition. However, HH gilts had greater backfat measurements on d 15 and at estrus than RH gilts.

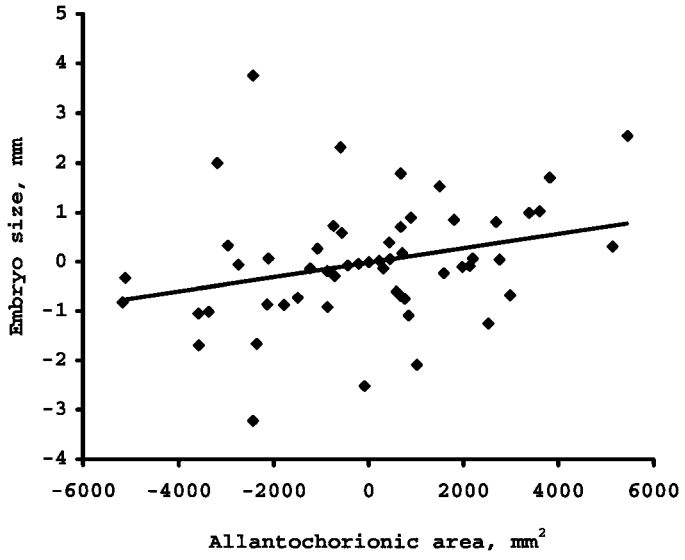

Figure 2. Relationship between residual embryo size (y-axis) and residual allantochorionic area (x-axis) after correction for block, treatment, and day. Embryo size and allantochorionic area are positively correlated (plot of residuals: embryo size = .0003 × (area) + 18.35, r = .28, $P = .03$).

Treatment affected embryonic survival rate at d 28 of pregnancy, without affecting ovulation rate. It has been established that the recruitment of preovulatory follicles occurs between d 14 and 16 of the porcine estrous cycle and coincides with luteolysis of the corpora lutea (Hunter and Wiesak, 1990). In addition, because the size of the proliferating pool of follicles may be an important determinant of ovulation rate,

factors that affect the size of this pool are of practical significance; genotype and nutrition have been clearly implicated (Clark et al., 1973; Dailey et al., 1975; Hunter et al., 1993). Other studies have also demonstrated effects of nutrition on ovulation rate. Cox et al. (1987) demonstrated an enhancement of ovulation rate in gilts by increasing dietary energy and administering insulin during the follicular phase. Consistent with these data, Flowers and coworkers (1989) reported that gilts provided additional dietary energy for at least 10 d prior to estrus ("flush feeding") exhibited greater ovulation rate. Furthermore, short-term changes in feed intake induce fluctuations in the energy status of the animal in the absence of major changes in body weight or composition (Booth, 1990).

Feeding the high plane of nutrition to the feed-restricted groups from d 16 of the cycle in the present study presumably allowed the gilts to recover from their less anabolic state, such that follicular recruitment into the preovulatory pool, and hence ovulation rate, were not affected by treatment. Furthermore, the level of feed restriction imposed was not severe (2.1 × maintenance), and even if feed had been restricted to ovulation it may not have markedly affected ovulation rate among groups.

Although ovulation rate was not affected, results from previous studies in lactating and weaned sows (Zak et al., 1997a,b), in which the restricted animals had an energy deficit of 25% compared with their counterparts fed for ad libitum intake, led us to hypothesize that a relative decrease in metabolic state late in the estrous cycle may still have a detrimental effect on subsequent fertility by affecting the status (maturation) of the ovarian follicles available for recruitment into the ovulatory population. Nutritionally dependent changes in intra-ovarian regulators of follicular function could, therefore, be a possible explanation for the low embryonic survival in the HR group, which was restricted during d 8 to 15 of the estrous cycle. Consistent with the studies in lactating and weaned sows (Zak et al., 1997a,b) and on the relationship between follicle status and oocyte maturation in the pig (Ding and Foxcroft, 1994), metabolic responses to feed restriction at critical stages of follicular growth in the estrous cycle may affect oocyte maturation and subsequent embryonic development. Direct evidence to support this possibility is being obtained using an extension of the experimental model used in the present study.

Furthermore, gilts that had the lowest embryonic survival rate at d 28 of pregnancy also had the lowest progesterone concentrations in early pregnancy (48 and 72 h after onset of estrus). Studies involving manipulation of feed intake around the time of estrus in gilts (Ashworth, 1991; Pharazyn et al., 1991; Jindal et al., 1996) or during lactation in sows (Baidoo et al., 1992; Zak et al., 1997a) also established differences in embryonic survival. Moreover, Ashworth (1991) and Jindal et al. (1997) demonstrated in gilts that progesterone injections in the early stages of pregnancy could counteract a nutritionally induced increase in embryonic loss. Thus, periovulatory progesterone could be the mediator of nutritionally induced effects on embryonic survival in gilts.

Studies in ewes have also suggested that the level of priming progesterone, modulated by pre-ovulatory nutrition, influenced embryo survival through direct effects on the developing oocyte (McEvoy et al., 1995a). In subsequent studies, McEvoy et al. (1995b) reported that the provision of supplementary progesterone to ewes on a high plane of feeding during the pre-ovulatory priming phase elevated plasma progesterone levels and enhanced subsequent ovum development.

This raises the additional possibility, previously discussed by Hunter and Wiesak (1990), that differences in follicular maturation before ovulation may be reflected in subtle but physiologically important differences in progesterone secretion in early pregnancy. The transient nature of the treatment-induced differences in plasma progesterone (48 and 72 h after onset of estrus) again confirms the importance of monitoring the patterns of progesterone secretion at critical times in early pregnancy (Foxcroft, 1997).

Variability in progesterone synthesis may lead to asynchrony between the embryo and uterus, and the time and pattern of the rise in plasma progesterone concentrations may be an important factor in determining the likelihood that an embryo will remain viable (Ashworth et al., 1989; Jindal et al., 1997). Therefore, the slower rise in progesterone levels in the HR gilts may be a cause of the lowest embryonic survival rate in this group.

As reported previously (Deligeorgis et al., 1984, 1985), our results showed that there were marked litter effects for some of the measurements analyzed, including age, body weight and backfat at first estrus (data not shown), ovulation rate, and placental area and volume. Hence, the use of littermates is highly recommended in such experiments to eliminate the effect of family and avoid biased results.

There is evidence that the development of d-28 conceptuses (embryos and their extra-embryonic membranes) is related to the extent of embryonic loss during the first 4 wk of pregnancy (Lutter et al., 1981). Hence, factors that are associated with embryonic mortality may also be associated with embryonic development. The uterus and its secretions mediate such effects, because embryos depend on uterine secretions for their development and they can only survive if the uterine environment develops in synchrony with their own development (Roberts and Bazer, 1988). However, the present results indicate that placental and embryonic size in the HR gilts with a higher embryonic mortality (32%) was not different from that in the groups with lower embryonic mortality (17%). Lack of placental development did not, therefore, seem to mediate nutritionally induced effects on embryonic survival to d 28 in this experimental paradigm. Indeed, placental

volume was negatively correlated to the number of surviving conceptuses, suggesting that when larger numbers of embryos survive the implantation process, uterine capacity may already be limiting placental growth. This is consistent with evidence from Biensen et al. (1998) that the uterine environment has a dominant effect on placental development up to d 90 of gestation. The data in Table 3 support previous evidence (see Foxcroft, 1997) that postimplantation loss of conceptuses may be the major component of prenatal loss in modern swine genotypes. The total number of pigs born to comparable gilts in our research herd is close to 10, indicating that of a total prenatal loss of up to 45% of ova ovulated, only 17% occurs in the preimplantation period, compared to 28% loss after d 28. The observed negative association between embryo numbers at d 28 and placental volume suggests that placental insufficiency may ultimately lead to subsequent loss of embryos in later gestation. If high embryonic survival rates to d 28 of gestation are typical of modern genotypes, and this is reflected in a trend toward smaller placental size in early pregnancy, the implications for both fetal birth weight and postnatal growth capacity merit careful evaluation.

Implications

The present study showed that different patterns of feed intake during the estrous cycle can be used to study effects on subsequent fertility. This will contribute to a better understanding of the interactions between nutrition and reproduction and to the nutritional management of breeding sow herds.

Literature Cited

Armstrong, J. D., and J. H. Britt. 1987. Nutritionally-induced anestrus in gilts: Metabolic and endocrine changes associated with cessation and resumption of estrous cycles. J. Anim. Sci. 65:508–523.

Ashworth, C. J. 1991. Effect of pre-mating nutritional status and post-mating progesterone supplementation on embryo survival and conceptus growth in gilts. Anim. Reprod. Sci. 26:311–321.

Ashworth, C. J., D. I. Sales, and I. Wilmut. 1989. Evidence of an association between the survival of embryos and the periovulatory plasma progesterone concentration in the ewe. J. Reprod. Fertil. 87:23–32.

Baidoo, S. K., F. X. Aherne, R. N. Kirkwood, and G. R. Foxcroft. 1992. Effect of feed intake during lactation and after weaning on sow reproductive performance. Can. J. Anim. Sci. 72:911–919.

Beltranena, E., G. R. Foxcroft , F. X. Aherne, and R. N. Kirkwood. 1991. Endocrinology of nutritional flushing in gilts. Can. J. Anim. Sci. 71:1063–1071.

Biensen, N. J., M. E. Wilson, and S. P. Ford. 1998. The impact of either a Meishan or Yorkshire uterus on Meishan or Yorkshire fetal and placental development to days 70, 90, and 110 of gestation. J. Anim. Sci. 76:2169–2176.

Bikker, P., M. W. A. Verstegen, B. Kemp, and M. W. Bosch. 1996. Performance and body composition of finishing gilts (45 to 85 kilograms) as affected by energy intake and nutrition in earlier life: I. Growth of the body and body components. J. Anim. Sci. 74:806–816.

Booth, P. J. 1990. Metabolic influences on hypothalamic-pituitary-ovarian function in the pig. In: Control of Pig Reproduction III. J. Reprod. Fertil. (Suppl.) 40:89–100.

Booth, P. J., J. Craigon, and G. R. Foxcroft. 1994. Nutritional manipulation of growth and metabolic and reproductive status in prepubertal gilts. J. Anim. Sci. 72:2415–2424.

Clark, J. R., T. N. Edey, N. L. First, A. B. Chapman, and L. E. Casida. 1973. Effects of four genetic groups and two levels of feeding on ovulation rate and follicular development in pubertal gilts. J. Anim. Sci. 36:1164–1169.

Cosgrove, J. R., J. E. Tilton, M. G. Hunter, and G. R. Foxcroft. 1992. Gonadotropin-independent mechanisms participate in ovarian responses to realimentation in feed-restricted prepubertal gilts. Biol. Reprod. 47:736–745.

Cox, N. M. 1997. Control of follicular development and ovulation rate in pigs. J. Reprod. Fertil. Suppl. 52:31–46.

Cox, N. M., M. J. Stuart, T. G. Althen, W. A. Bennet, and H. W. Miller. 1987. Enhancement of ovulation rate in gilts by increasing dietary energy and administering insulin during follicular growth. J. Anim. Sci. 64:507–516.

Dailey, R. A., J. R. Clark, N. L. First, A. B. Chapman, and L. E. Casida. 1975. Loss of follicles during the follicular phase of the estrous cycle of swine as affected by genetic group and level of feed intake. J. Anim. Sci. 41:835–841.

Deligeorgis, S. G., P. R. English, and G. A. Lodge. 1985. Interrelationship between growth, gonadotrophin secretion and sexual maturation in gilts reared in different litter sizes. Anim. Prod. 41:393–401.

Deligeorgis, S. G., P. R. English, G. A. Lodge, and G. R. Foxcroft. 1984. Comparison of two methods for evaluating reproductive development in prepubertal gilts. Anim. Prod. 38:283–291.

Ding, J., and G. R. Foxcroft. 1994. Epidermal growth factor enhances oocyte maturation in pigs. Mol. Reprod. Dev. 39:30–40.

Flowers, B., M. J. Martin, T. C. Cantley, and B. N. Day. 1989. Endocrine changes associated with a dietary-induced increase in ovulation rate (flushing) in gilts. J. Anim. Sci. 67:771–778.

Foxcroft, G. R. 1997. Mechanisms mediating nutritional effects on embryo survival in pigs. J. Reprod. Fertil. (Suppl.) 52:47–61.

Foxcroft, G. R., F. X. Aherne, E. C. Clowes, H. Miller, and L. J. Zak. 1995. Sow fertility: The role of suckling inhibition and metabolic status. In: M. Ivan (Ed.) Animal Science Research and Development: Moving Toward a New Century. pp.377-393, Centre of Food and Animal Research, Ottawa, Canada.

Hunter, M. G., C. Biggs, G. R. Foxcroft, A. S. McNeilly, and J. E. Tilton. 1993. Comparisons of endocrinology and behavioural events during the periovulatory period in Meishan and Large-White hybrid gilts. J. Reprod. Fertil. 97:475–480.

Hunter, M. G., and T. Wiesak. 1990. Evidence for and implications of follicular heterogeneity in pigs. J. Reprod. Fertil. (Suppl.) 40:163–177.

Jindal, R., J. R. Cosgrove, F. X. Aherne, and G. R. Foxcroft. 1996. Effect of nutrition on embryonal mortality in gilts: Association with progesterone. J. Anim. Sci. 74:620–624.

Jindal, R., J. R. Cosgrove, and G. R. Foxcroft. 1997. Progesterone mediates nutritionally induced effects on embryonic survival in gilts. J. Anim. Sci. 75:1063–1070.

Koketsu, Y. 1994. Influence of feed intake and other factors in the lactational and postweaning reproductive performance of sows. Ph.D. thesis, Univ. of Minnesota, St. Paul.

Lutter, K., R. Hühn, U. Hühn, U. Kaltofen, B. Lampe, and F. Schneider. 1981. Untersuchungen zum pränatalen Fruchttod bei Jungsauen sowie zum Wachstum der embryonen und Feten. Arch. Exp. Vet. Med. 35:687–695.

Mao, J., and G. R. Foxcroft. 1998. Progesterone therapy during early pregnancy and embryonic survival in primiparous weaned sows. J. Anim. Sci. 76:1922–1928.

McEvoy T. G., J. J. Robinson, R. P. Aitken, P. A. Findlay, R. M. Palmer, and I. S. Robertson. 1995a. Dietary-induced suppression of pre-ovulatory progesterone concentrations in superovulated ewes impairs the subsequent in vivo and in vitro development of their ova. Anim. Reprod. Sci. 39:89–107.

McEvoy, T. G., J. J. Robinson, R. P. Aitken, P. A. Findlay, and I. S. Robertson. 1995b. Relationship between pre-ovulatory feed intake, progesterone priming and the subsequent in vitro development of ova collected from superovulated ewes. Theriogenology 43:276.

Morbeck, D. E., K. L. Esbenshade, W. L. Flowers, and J. H. Britt. 1992. Kinetics of follicle growth in the prepubertal gilt. Biol. Reprod. 47:485–491.

NRC. 1988. Nutrient Requirements of Swine (9th Ed.). National Academy Press, Washington, DC.

NRC. 1998. Nutrient Requirements of Swine (10th Ed.). National Academy Press, Washington, DC.

Pharazyn, A., G. R. Foxcroft, and F. X. Aherne. 1991. Temporal relationship between plasma progesterone concentrations in the utero-ovarian and jugular veins during early pregnancy in the pig. Anim. Reprod. Sci. 26:323–332.

Roberts, R. M., and F. W. Bazer. 1988. The functions of the uterine secretions. J. Reprod. Fertil. 82:875–892.

SAS. 1990. SAS User's Guide: Statistics (Version 6.06 Ed.). SAS Inst. Inc., Cary, NC.

Williams, J. P. G., J. M. Tanner, and P. C. R. Hughes. 1974. Catch-up growth in female rats after growth retardation during suckling period: Comparison with males. Pediatr. Res. 8:157–162.

Zak, L. J., J. R. Cosgrove, F. X. Aherne, and G. R. Foxcroft. 1997a. Pattern of feed intake and associated metabolic and endocrine changes differentially affect postweaning fertility in primiparous lactating sows. J. Anim. Sci. 75:208–216.

Zak, L. J., X. Xu, R. T. Hardin, and G. R. Foxcroft. 1997b. Impact of different patterns of feed intake during lactation in the primiparous sow on follicular development and oocyte maturation. J. Reprod. Fertil. 110:99–106.