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Level of dietary energy during prepubertal growth and reproductive development of gilts[1,2]

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ABSTRACT: Development of gilts that conceive early and continue to produce offspring is a primary objective of swine production. The objective of this study was to determine the degree of feed restriction during development required to optimize reproductive performance and efficiency in gilts. The effects that various patterns of growth had on reproductive development and performance of gilts through d 30 of gestation were investigated. At 13 wk of age and 41 kg BW, 192 white crossbred gilts were penned individually and assigned to receive 87.5%, 75%, 62.5%, and 50% of predicted ad libitum energy intake. The study was replicated in two seasons. At 25 wk of age, gilts were moved to group pens and allowed ad libitum access to feed, and estrous detection was initiated. Gilts were inseminated at first observed estrus and those recycling were remated. Postmating gilts were fed 1.5× maintenance in stalls. Gilts that did not return to estrus 17 to 30 d after mating were slaughtered at 30 d of gestation. Reproductive tracts were collected and numbers of corpora lutea and live embryos were recorded. Feed restriction during development resulted in differences in BW and backfat thickness at the start of the breeding period and differences in feed intake during breeding. Gilts subjected to the greatest feed restriction during development consumed the greatest quantity of feed during breeding. Feed intake during breeding was associated with BW and backfat gain during breeding. The treatment group that entered breeding lightest and leanest (50% of predicted ad libitum intake) had the least number of days to first estrus, followed by the fattest, heaviest group (87.5% of predicted ad libitum intake). Treatment groups did not differ ($P > 0.38$) in ovulation rate or live embryo numbers. Significant relationships between quantity of GE consumed during development and variables considered important in reproductive development and performance were evident, such as BW and fatness at start of breeding and first detected estrus, and ovulation rate. Variation in dietary energy during the development period impacted many aspects of reproductive development and performance. However, coupling restricted energy intake during development with ad libitum intake during breeding negated many of the effects of feed restriction during the development period.

Key Words: Gilts, Growth, Pregnancy, Puberty

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Introduction

Adequate nutrition during growth is required for normal development of reproductively competent females. We have reported that gilts subjected to moderate (74% of ad libitum) dietary restriction during the prepubertal period exhibited similar age at first estrus and reproductive performance as gilts fed as recommended (Reese et al., 1995) or ad libitum (Klindt et al., 1999; Klindt et al., 2001). In contrast, Beltranena et al. (1991), reported decreased BW at the start of breeding and increased age at first estrus in gilts fed a restricted quantity of feed through first estrus when compared with ad libitum fed gilts. In a production environment, there is a positive relationship between BW at 180 d of age and percentage of gilts exhibiting estrus (Stalder and Goodwin, 2000). Although some gilts in the previous study (Klindt et al., 1999) were subjected to moderate dietary restriction during growth, and had 13% less BW at start of breeding, all gilts were fed ad libitum during breeding. This ad libitum feeding during breeding induced previously restricted gilts to consume greater quantities of feed during the early portion of the breeding period than were consumed by gilts fed as recommended during development.

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We hypothesize that increased feed intake resulted in greater metabolic rate and organ growth, which compensated for the deleterious effects of feed restriction during development, resulting in similar reproductive performance in all groups of gilts through 30 d of gestation. Reduced feed intake combined with similar reproductive output resulted in greater numbers of embryos produced through 30 d of gestation per unit of feed fed in moderately restricted gilts.

The objective of this study was to determine the degree of feed restriction during a 12-wk growth and development period when followed by ad libitum feed availability during breeding that would optimize reproductive performance in gilts.

Materials and Methods

Crossbred white (American Landrace × Yorkshire) gilts were used in the study. The study was replicated with gilts born in two farrowing groups. Selected litters contained at least four gilts. Average birth dates were January 13 (SD = 3.8 d, n = 96) and July 12 (SD = 4.6 d, n = 96). Gilts for the study were selected at approximately 12 wk of age and were assigned to four developmental feeding regimens that were imposed from 13 to 25 wk of age. The four treatments were as follows: ½Adlib, fed 50% of predicted ad libitum intake; ⅝Adlib, fed 62.5% of predicted ad libitum intake; ¾Adlib, fed 75% of predicted ad libitum intake; and ⅞Adlib, fed 87.5% of predicted ad libitum intake. The experimental design was a randomized block with litter as the blocking criterion. Predicted ad libitum intake was calculated with an equation derived from recorded ad libitum intake of similar corn-soybean meal diets by gilts of this population in the same facilities in previous studies (Klindt et al., 1999; Klindt et al., 2001): ad libitum intake in grams per kilogram of $BW^{0.75} = 201.654 - (1.4669 \times BW) + (0.00455 \times BW^2)$. The gilts were weighed at 2-wk intervals, and predicted ad libitum intake was calculated using predicted BW midway into the 2-wk period for which the feed level was calculated. Corn-soybean meal diets were formulated to meet National Research Council (NRC, 1988) recommendations for protein, minerals, and vitamins at the predicted intakes (Table 1). Because the diets were formulated with similar energy densities, concentrations of protein, minerals, and vitamins were adjusted to obtain the required intakes of these components with less feed intake (Table 1). At the 2-wk weighings, backfat thickness was determined ultrasonically (Lean-Meater, Renco Corp., Minneapolis, MN) from 5 to 8 cm off the midline at the first rib, last rib, and last lumbar vertebrae, and these three measures were averaged to obtain average backfat thickness. During development, gilts were housed in individual pens (1.2 × 1.2 m) in an enclosed temperature-controlled building (~21°C, SD = 3.6) with free access to water. All animal procedures were reviewed and approved by the U.S. Meat Animal Research Center Animal Care and Use Committee.

At an average age of 25 wk (end of the development period), gilts were transported to a breeding facility and placed in group pens (2.44 × 6.40 m) and all gilts were offered a breeding and gestation diet (Table 1) ad libitum in self-feeders (1.22 m, five holes). These pens are subsequently referred to as *estrus detection*, or *breeding pens*. Gilts were group-penned by heavier and lighter weight within treatment group (two pens per treatment group). Initially, there were 12 gilts per pen, 1.3 m^2/gilt. In the breeding pens, gilts used self-feeders. The quantity of feed offered and a census of each pen was recorded daily. Gilts were weighed and backfat thickness was determined by ultrasound weekly. Bred gilts were weighed and backfat was determined at the first weigh day after each mating.

In the breeding facility, morning estrus checks were performed with mature, experienced intact boars using fence-line exposure for 15 min. The first detected estrus after the initiation of boar exposure and estrus checks was considered the pubertal estrus. Gilts detected in estrus were moved to stalls and inseminated that afternoon and again the following morning with 100 mL of diluted (Androhep-Long Term, Minitube of America, Verona, WI) mixed semen from at least two crossbred white (American Landrace × Yorkshire) boars. Semen was used within 72 h of collection. Each insemination was with 6 to 8 × 10^9 total sperm. Beginning 17 d after mating, gilts were checked for estrus daily by running the boar in front of the crates for 15 min and those gilts returning to estrus were inseminated again, as previously described. Pregnant gilts were slaughtered at 30 (28 to 32) d of gestation. At slaughter, reproductive tracts were collected and the number of corpora lutea (CL) on each ovary and the total number and number of live embryos in each uterine horn were recorded. Gilts that did not exhibit estrus by d 77 of the breeding period (~252 d of average age) and bred gilts that recycled after d 77 of the breeding period were sold for slaughter and reproductive tracts were not available for examination. In stalls, gilts were fed the breeding and gestation diet (Table 1) at 158 kcal ME/kg $BW^{0.75}$ (Jindal et al., 1996), that is, ~1.8 kg feed/125 kg gilt, based on calculated ME of the diet.

Statistical analyses of the results were performed using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC). For analysis of most variables, all gilts assigned to the study were included. Thus, zeros were included as valid observations in some analyses, such as, total feed intake during breeding and early gestation, numbers of CL, number of embryos, and embryo efficiency (number of embryos at 30 d per kilogram of feed consumed from 13 wk of age to 30 d of gestation). Exceptions were made when the inclusion of all gilts resulted in invalid observations for the variable, for example, days to first estrus. Analysis of treatment group effects included the random effect of litter within farrowing group or replicate. Average daily gain and average daily change in backfat thickness for each animal were determined by linear regression. Differences among means were compared using a

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Table 1. Compositions of feed given to gilts throughout the trial and the calculated intake of nutrients

	Development period treatment[a]									
Treatment group:	⅞Adlib			¾Adlib			⅝Adlib		½Adlib	All gilts
stage or period:[b] Item	13 wk to 60 kg	60 to 80 kg BW	80 kg BW to 25 wk	13 wk to 60 kg BW	60 to 80 kg BW	80 kg BW to 25 wk	13 wk to 60 kg BW	60 kg to 25 wk	13 wk to 25 wk	Breeding and gestation
Calculated nutrient composition										
DM, %	88.62	88.49	88.43	88.81	88.66	88.59	89.08	88.91	89.50	88.83
CP, %[c]	13.60	12.80	12.00	15.87	14.93	14.00	19.04	18.00	23.80	12.83
Fat, crude, %	3.75	3.43	3.36	4.03	3.66	3.58	4.42	3.98	5.03	4.83
Fiber, crude, %	3.31	3.24	3.16	3.56	3.47	3.39	3.90	3.81	4.42	3.74
Calcium, %	0.75	0.65	0.65	0.88	0.76	0.76	1.05	0.91	1.31	0.95
P, %	0.64	0.55	0.55	0.71	0.61	0.61	0.81	0.69	0.97	0.81
P, available, %	0.38	0.30	0.30	0.44	0.35	0.35	0.53	0.42	0.67	0.55
Digestible cystine, %[d]	0.16	0.15	0.14	0.18	0.17	0.16	0.22	0.21	0.27	0.15
Digestible lysine, %[e]	0.72	0.63	0.54	0.83	0.74	0.63	1.00	0.88	1.25	0.43
Digestible methionine, %	0.33	0.30	0.24	0.38	0.36	0.28	0.46	0.43	0.57	0.20
Digestible tryptophan, %	0.17	0.16	0.14	0.20	0.18	0.17	0.24	0.23	0.30	0.12
Digestible Met + Cys, %	0.48	0.45	0.38	0.56	0.53	0.44	0.68	0.63	0.84	0.35
ME, Mcal/kg	3.30	3.30	3.30	3.30	3.30	3.30	3.03	3.30	3.30	3.30
Analyzed composition (as fed)[f]										
DM, %	87.5	87.8	87.2	87.9	87.6	87.7	88.3	87.7	88.6	85.2
Ash, %	4.42	4.48	3.84	5.05	4.73	4.47	5.96	5.31	7.63	6.17
CP, %	13.5	13.1	11.7	15.7	14.9	13.4	18.0	17.4	22.0	13.7
Gross energy, Mcal/kg	3.80	3.80	3.79	3.86	3.84	3.82	3.87	3.84	3.88	4.27
Calculated consumption[g]										
No. of days fed	30	22	32	33	30	21	42	42	84	—
Intake (as fed), kg/d	2.32	2.59	2.79	1.97	2.22	2.37	1.64	1.89	1.38	—
Ash, kg/d	0.103	0.116	0.107	0.099	0.105	0.106	0.098	0.100	0.105	—
CP, kg/d	0.314	0.338	0.326	0.309	0.330	0.319	0.296	0.329	0.304	—
GE, Mcal/d	8.82	9.84	10.57	7.60	8.52	9.06	6.36	7.26	5.36	—

[a]Development period treatments imposed from 13 to 25 wk of age: ⅞Adlib, 87.5% of predicted ad libitum intake; ¾Adlib, 75% of predicted ad libitum intake; ⅝Adlib, 62.5% of predicted ad libitum intake; and ½Adlib, 50% of predicted ad libitum intake.
[b]Stage or period identified as the age in weeks or BW in kilograms during which the diet was fed.
[c]Assuming the CP content is 8.5% for corn and 44% for soybean meal (NRC, 1988).
[d]Digestible amino acid values based on apparent digestibilities (NRC, 1988).
[e]Assuming the lysine content is 0.255% for corn and 2.9% for soybean meal (NRC, 1988).
[f]AOAC, (1984).
[g]Calculated from average daily feed intake during development period and analyzed nutrient composition.

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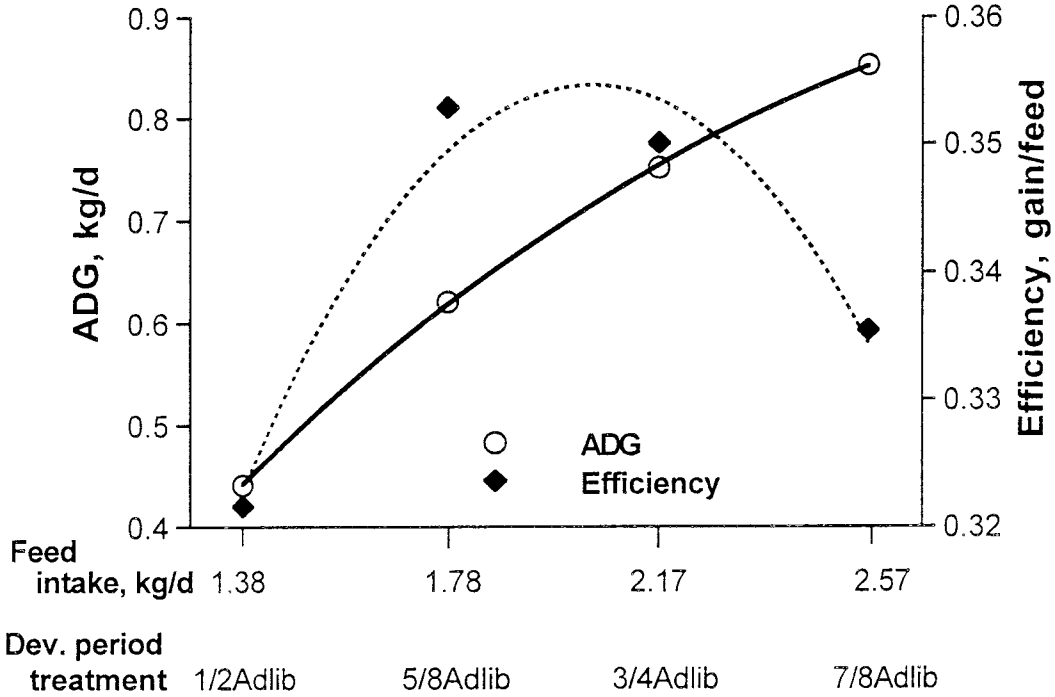

Figure 1. Influence of feed intake from 13 to 25 wk of age on the rate of gain and efficiency of gain in developing gilts. Gilts assigned to the ½Adlib, ⅝Adlib, ¾Adlib, and ⅞Adlib treatments were fed 50, 62.5, 75, and 87.5% of predicted ad libitum intake, respectively. The solid line presents the second-order polynomial for ADG, ADG = $-0.449 + (0.861 \times \text{feed intake}) + [-0.130 \times (\text{feed intake})^2]$. Broken line presents second order polynomial equation for efficiency, efficiency = $0.049 + (0.300 \times \text{feed intake}) + [-0.074 \times (\text{feed intake})^2]$. The fitted equation predicts maximal feed efficiency would be 0.353 at a feed intake of 2.03 kg/d.

protected *t*-test considering an alpha for treatment of less than or equal to 0.05 as significant. The regression analyses were performed using a continuous variable, that is, measured daily GE intake during development period, BW at initiation of estrus detection (25 wk of age), and day of first estrus, as the independent variable. Step-down analysis of variance was performed using a minimal error mean square criterion (Klindt et al. 1985).

Results

At the beginning of the trial, gilts were 91.5 ± 4.2 (SD) d of age, were 40.7 ± 5.8 (SD) kg BW, and had 10.9 ± 1.5 (SD) mm average backfat thickness. During the 12-wk growth and development period, gilts assigned to the ½Adlib, ⅝Adlib, ¾Adlib, and ⅞Adlib groups consumed 5.4, 6.8, 8.3, and 9.8 Mcal GE/d, respectively. These feed levels resulted in a near linear change in rate of gain from 13 to 25 wk of age (Figure 1). Greatest efficiencies of gain were with the ⅝Adlib and ¾Adlib feed levels. At the end of the development period, BW ranged from 78 to 113 kg and backfat thickness ranged from 12 to 23 mm (Table 2) for the treatment groups.

At 25 wk of age, gilts were moved to the breeding facility and given ad libitum access to feed. Feed consumption in the breeding facility was inversely related to quantity fed during the development period. Gilts fed at the highest level during the development period had the lowest rate of feed consumption during the breeding period, 3.06 kg/d, whereas those fed the least during development had the highest rate of feed consumption during breeding, 3.76 kg/d (Table 3). Average daily feed consumption during breeding exceeded the quantity of feed offered during the last 2 wk of development for all treatment groups. Quantity of feed offered during the last 2 wk of the development period was 1.49, 1.94, 2.37 and 2.82 kg/d for the ½Adlib, ⅝Adlib, ¾Adlib and ⅞Adlib groups, respectively. Rates of gain in BW and average backfat thickness during the breeding period (Table 2) were positively related to rate of feed consumption during breeding and consequently were inversely related to level of feed offered during development (Table 3).

Feed consumption and rates of BW and backfat gain were associated with onset of estrus (Table 2, Figure 2). Average number of days from entry into the breeding facility to the first detected estrus was least in ½Adlib gilts, followed by ⅞Adlib gilts, and was greatest in ⅝Adlib and ¾Adlib gilts ($P < 0.01$). Age at establishment of pregnancy followed a similar pattern (Table 2). About 84% of the gilts assigned to the study showed estrus and 76% became pregnant during the 77-d breeding period (Table 2). The number of embryos produced per gilt, whether divisor is gilt assigned, pubertal, or pregnant, was not influenced ($P > 0.38$) by treatment (Table 2). However, treatment influenced ($P < 0.01$) efficiency of live embryo production, with the greatest efficiency in

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the ½Adlib group and the least in the ⅞Adlib group (Table 3). Although development period treatment did not affect ovulation rate (Table 2), ovulation rate changed with week of conception ($P < 0.01$, Figure 3). Ninety-two percent of the gilts that became pregnant did so at the first observed estrus. Number of live embryos at 30 d of gestation was not influenced by estrus of successful insemination ($P > 0.17$).

Variation in energy intake during the development period was related to gain during development (Figure 4). Daily GE intake during the development period was distributed between 5.0 and 10.6 Mcal/d. Daily GE in-

Table 2. Body weight and average backfat thickness measurements and reproductive performance in gilts fed at different levels during the prepubertal development period[a]

	Development period treatment[b]					
Basis of analysis trait	½Adlib	⅝Adlib	¾Adlib	⅞Adlib	PSE[c]	Trt *P*-value[d]
All gilts assigned						
No. of gilts	48	48	48	48	—	—
BW at start of breeding, 25 wk of age, kg	77.8[e]	92.8[f]	103.7[g]	112.7[h]	0.5	0.01
Avg backfat at start of breeding, mm	12.0[e]	15.7[f]	19.5[g]	23.0[h]	0.2	0.01
Total number of embryos/gilt	9.0	8.8	9.0	7.9	0.4	0.77
Live embryos/gilt	8.9	8.4	8.6	7.8	0.4	0.77
Pubertal gilts						
No. of gilts	41	38	42	41	—	—
% pubertal[i]	85.4	79.2	87.5	85.4	—	—
Day of breeding pubertal	15.3[e]	24.5[f]	27.9[f]	22.4[df]	1.3	0.01
BW at start of breeding, kg	77.9[e]	93.1[f]	103.2[g]	113.0[h]	0.5	0.01
BW at puberty, kg	93.1[e]	110.8[f]	120.0[g]	122.7[g]	1.1	0.01
ADG, 25 wk of age to puberty, kg	0.974[e]	0.757[f]	0.519[g]	0.389[g]	0.025	0.01
Avg backfat at start of breeding, mm	12.1[e]	15.6[f]	19.6[g]	23.1[h]	0.2	0.01
Avg backfat at puberty, mm	16.4[e]	21.2[f]	24.8[g]	25.4[g]	0.3	0.01
Daily change in Avg backfat, 25 wk to puberty, mm	0.291[e]	0.234[e]	0.217[e]	0.111[f]	0.017	0.01
Total number of embryos/gilt	10.4	11.1	10.3	9.2	0.4	0.39
Live embryos/gilt	10.3	10.6	9.9	9.0	0.4	0.47
Pregnant gilts						
No. of gilts	37	37	37	35	—	—
% pregnant at 30 d	77.1	77.1	77.1	72.9	—	—
Day pregnant	17.7[e]	24.7[e]	29.7[f]	25.3[e]	1.4	0.03
BW at start of breeding, kg	78.1[e]	93.1[f]	102.4[g]	112.3[h]	0.6	0.01
BW at pregnancy, kg	90.5[e]	108.9[f]	116.7[g]	123.1[g]	1.3	0.01
ADG, 25 wk of age to pregnancy, kg	0.868[e]	0.746[e]	0.476[f]	0.405[f]	0.037	0.01
Avg backfat at start of breeding, mm	12.1[e]	15.6[f]	19.5[g]	23.4[h]	0.2	0.01
Avg backfat at pregnancy, mm	15.9[e]	20.9[f]	24.2[g]	26.2[g]	0.371	0.01
Daily change in Avg backfat, 25 wk to pregnancy, mm	0.271	0.234	0.233	0.131	0.019	0.06
Ovulation rate, corpora lutea/gilt	13.8	14.6	13.9	13.8	0.2	0.40
Total number of embryos/gilt	11.3	11.4	11.6	10.9	0.3	0.84
Live embryos/gilt	11.2	11.0	11.2	10.6	0.3	0.90

[a]For rows in which a pooled standard error (PSE) and probability value are presented, the treatment values are least-squares means.

[b]Development period treatments imposed from 13 to 25 wk of age: ½Adlib, 50% of predicted ad libitum intake; ⅝Adlib, 62.5% of predicted ad libitum intake; ¾Adlib, 75% of predicted ad libitum intake; and ⅞Adlib, 87.5% of predicted ad libitum intake.

[c]Pooled standard error.

[d]Probability that there is no differences among the least-squares means within a row.

[e,f,g,h]Means within a row with common superscripts are not different, $P < 0.05$.

[i]Puberty is defined as first detected estrus after initiation of boar exposure and estrus detection at 25 wk of age.

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Table 3. Means for feed intake during the phases of gilt development and efficiency of production of 30-d-old embryos in gilts fed different levels during prepubertal development[a]

	Development period treatment[b]					
Basis of analysis trait	½Adlib	⅝Adlib	¾Adlib	⅞Adlib	PSE[c]	Trt *P*-value[d]
All gilts assigned						
No. gilts assigned	48	48	48	48	—	—
Breeding period feed, kg	82.6	110.1	107.8	90.7	6.1	0.32
Breeding period feed, kg·gilt^{-1}·day^{-1}	3.76[e]	3.28[f]	3.19[f]	3.06[e]	0.05	0.01
Feed in gestation stalls, kg	40.8	42.0	46.6	51.8	1.7	0.08
Feed in gestation stalls, kg·gilt^{-1}·day^{-1}	1.24[e]	1.31[f]	1.55[f]	1.51[f]	0.05	0.05
Total feed, 13 wk of age to 30 d gestation, kg	240.4[e]	301.3[f]	336.5[g]	358.0[g]	5.5	0.01
Live embryos at 30 d of gestation, no.	8.9	8.4	8.6	7.8	0.4	0.77
Live embryos at 30 d of gestation/kg total feed	0.0407[e]	0.0298[f]	0.0273[e]	0.0230[e]	0.0014	0.01
Pubertal gilts						
No. gilts pubertal	41	38	42	41	—	—
Breeding period feed, kg	58.3[e]	83.2[e]	94.5[f]	66.8[e]	4.5	0.02
Breeding period feed, kg·gilt^{-1}·day^{-1}	3.87[e]	3.45[e]	3.32[f]	3.08[g]	0.03	0.01
Feed in gestation stalls, kg	47.8[e]	52.5[e]	53.4[e]	60.4[f]	1.1	0.01
Feed in gestation stalls, kg·gilt^{-1}·day^{-1}	1.46[e]	1.66[f]	1.78[g]	1.78[g]	0.01	0.01
Total feed, 13 wk of age to 30 d gestation, kg	222.2[e]	285.4[f]	329.7[g]	343.3[g]	4.8	0.01
No. of live embryos at 30 d of gestation	10.3	10.6	9.9	9.0	0.4	0.47
Live embryos at 30 d of gestation/kg total feed	0.0469[d]	0.0379[e]	0.031[ef]	0.0268[f]	0.0010	0.01
Pregnant gilts						
No. gilts pregnant	38	37	35	32	—	—
Breeding period feed, kg	61.0[e]	79.7[df]	97.7[f]	73.4[df]	4.7	0.04
Breeding period feed, kg·gilt^{-1}·day^{-1}	3.89[e]	3.44[f]	3.31[f]	3.08[g]	0.03	0.01
Feed in gestation stalls, kg	46.7[e]	52.1[f]	53.5[f]	54.8[f]	0.1	0.01
Feed in gestation stalls, kg·gilt^{-1}·day^{-1}	1.47[e]	1.65[f]	1.78[f]	1.78[g]	0.01	0.01
Total feed, 13 wk of age to 30 d gestation, kg	224.0[e]	281.5[f]	332.6[g]	343.8[g]	5.0	0.01
Live embryos at 30 d of gestation, no.	11.2	11.0	10.9	10.4	0.6	0.83
Live embryos at 30 d of gestation/kg total feed	0.0507[e]	0.0393[f]	0.0343[f]	0.0307[g]	0.0011	0.01

[a]Least-squares means.
[b]Development period treatments imposed from 13 to 25 wk of age: ½Adlib, 50% of predicted ad libitum intake; ⅝Adlib, 62.5% of predicted ad libitum intake; ¾Adlib, 75% of predicted ad libitum intake; and ⅞Adlib, 87.5% of predicted ad libitum intake.
[c]Pooled standard error.
[d]Probability that there are no differences among the means within a row.
[e,f,g]Means in a row with common superscripts are not different, $P < 0.05$.

take was related ($P < 0.05$) to most measures (Table 4). Exceptions were days to first estrus after entering the breeding facility, daily gain in backfat thickness from 25 wk of age to first estrus, days after entering the breeding facility the gilt became pregnant, daily gain in backfat thickness from 25 wk of age to pregnancy, and number of CL and live embryos at 30 d of gestation. When various measures were regressed on BW at 25 wk of age, nonsignificant ($P > 0.05$) relationships were present for days to first estrus and pregnancy, daily gain in backfat thickness to puberty and pregnancy, and number of live embryos at 30 d of gestation (Table 4). Number of days from entry into the breeding facility until first estrus was detected was not related to ADG from start of breeding to first estrus or pregnancy, daily gain in backfat thickness to first estrus and pregnancy, or number of live embryos at 30 d of gestation (Table 4). The regression of efficiency of embryo production (live embryos at 30 d

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of gestation per kilogram of total feed) on pubertal day was not significant.

Discussion

The objective of gilt development is to produce females that become pubertal, become pregnant, and enter the sow herd at an early age and produce an economically viable number of offspring and maintain efficient lifetime productivity. Dietary energy restriction during prepubertal development influenced days to first estrus and pregnancy. The treatment group that was fed the lowest quantity of feed during prepubertal development exhibited estrus earliest followed by the group fed the largest quantity of feed during prepubertal development. Development period dietary energy intake had no impact on number of 30-d-old live embryos produced. However, the efficiency of conversion of feed to 30-d-old live embryos was negatively related to quantity of dietary energy fed during the development period.

Previously, other workers (Beltranena et al., 1991) have investigated the influence of restricted feeding through the first or pubertal estrus on development of gilts. They reported a negative impact of restricted feeding on age at puberty, ovulation rate, and number of embryos. In the present study, gilts were restricted from 13 wk of age until moved to the breeding facility at 25 wk of age and, in contrast to the studies of Beltranena et al. (1991), all gilts were given ad libitum access to feed in the breeding facility. In the present study, there was a nonlinear inverse relationship between level of dietary energy fed during development and days to puberty with no effect on ovulation rate or number of embryos. Ad libitum access to feed during the breeding period contravened the negative effects of dietary energy restriction during the 12-wk prepubertal development period, particularly in the ½Adlib group. Compensatory gains exhibited by the previously restricted gilts during the early portion of the breeding period may have been responsible for this response.

Recent reports present evidence that gilts with reduced BW at the start of breeding are slower to exhibit first estrus and become pregnant (Stalder and Goodwin, 2000; Stalder et al., 2000). In those reports, gilts that weighed less were lighter due to a unique characteristic of the individual gilt's physiology or some specific uncontrolled interaction of the gilt with her environment. The lighter-weight gilts in the current study were nutritionally managed to have less BW at the start of breeding. Stalder et al. (2000) and Stalder and Goodwin (2000) did not allow ad libitum feed consumption and compensatory gains in the light-weight gilts. Therefore, those gilts were slower to exhibit first estrus and become pregnant than their heavier contemporaries. Lighter gilts in the current study exhibited the greatest ad libitum feed consumption in the breeding facility and greater BW

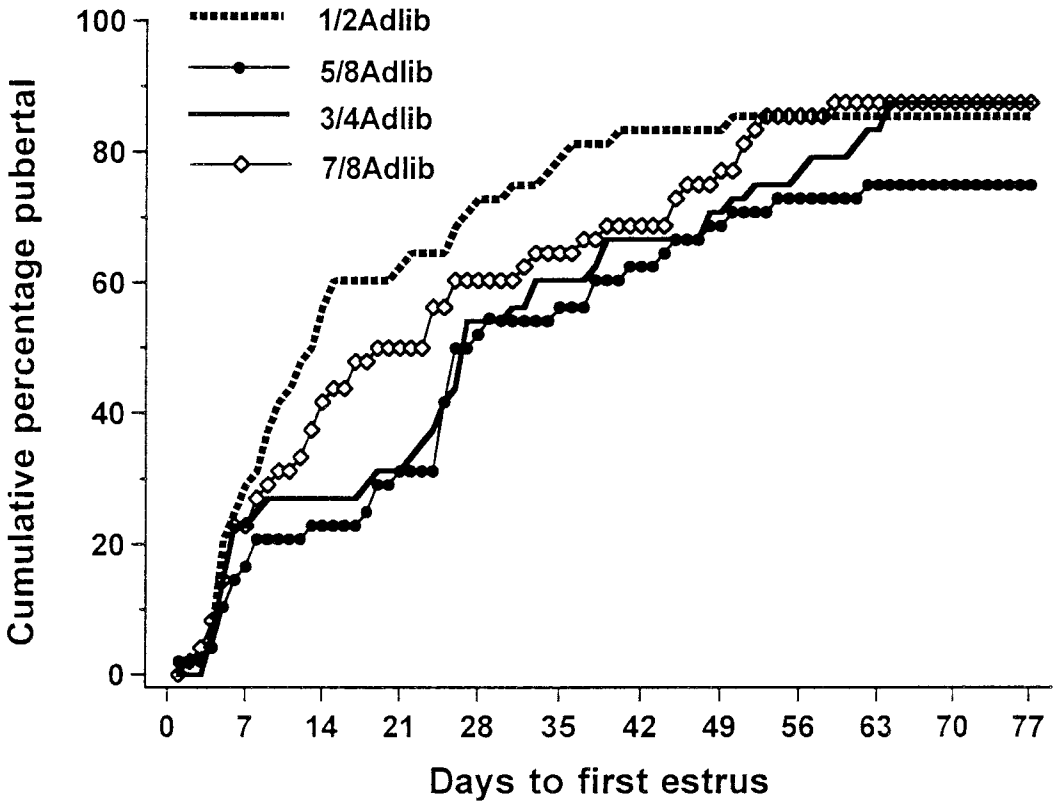

Figure 2. Cumulative percentage of gilts exhibiting estrus during the breeding period. Forty-eight gilts in two replicates were assigned to each treatment group.

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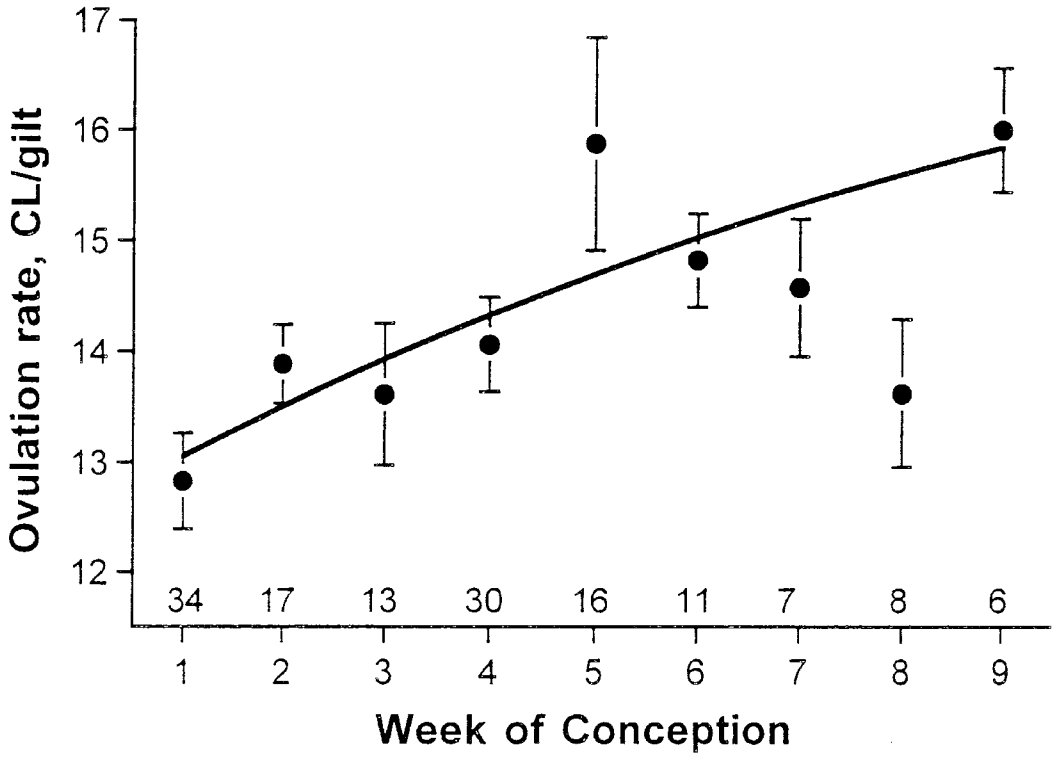

Figure 3. Effect of week of breeding when gilts became pregnant on for ovulation rate ($P < 0.01$) (CL = corpora lutea). Points are weekly means (± SE). Numbers above the ordinate present the number of gilts that became pregnant during that week. The effects of treatment ($P > 0.90$) and the interaction of treatment week pregnant ($P > 0.12$) were not significant.

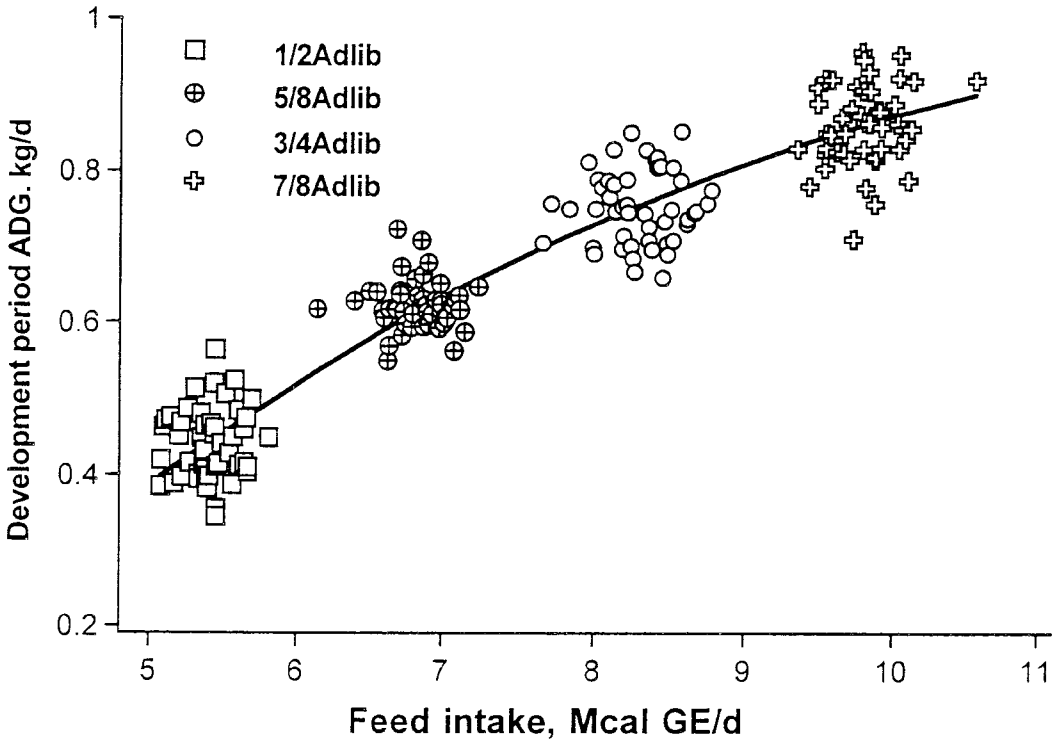

Figure 4. Relationship among feed intake and ADG during development period. The equation for the fitted line is $-0.518 + (0.223 \times \text{feed intake}) + [-0.008 \times (\text{feed intake})^2]$.

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Table 4. Regression of traits possibly important in reproductive development on daily GE intake during development, BW at start of the breeding period and days to first estrus[a]

Item	No. of observations	Intercept[b]	$\beta 1$ Estimate	$\beta 1$ SE Est.	$\beta 1$ *P*-value[c]	$\beta 2$ Estimate	$\beta 2$ SE Est.	$\beta 2$ *P*-value[c]	R^2
Independent variable: Daily GE intake during development period									
Dependent variable									
25 wk of age wt, kg	192	0.95	17.71	2.17	0.01	–0.64	0.14	0.01	0.94**
25 wk backfat thickness, mm	192	–3.57	3.12	1.02	0.01	–0.04	0.07	0.54	0.87**
Day of breeding pubertal	162	–97.19	31.51	9.13	0.01	–1.97	0.60	0.01	0.36
Pubertal wt, kg	162	–31.23	32.27	7.10	0.01	–1.70	0.46	0.01	0.66**
Pubertal backfat thickness, mm	162	–20.44	9.50	2.22	0.01	–0.49	0.14	0.01	0.66**
ADG 25 wk to puberty, kg	162	2.62	–0.39	0.17	0.03	0.016	0.011	0.14	0.62**
Daily backfat gain 25 wk to puberty, mm	162	0.19	0.05	0.11	0.64	–0.006	0.007	0.41	0.38
Day of breeding pregnant	146	–76.18	25.44	9.91	0.02	–1.53	0.65	0.02	0.40
Pregnancy wt, kg	146	12.13	20.76	9.19	0.03	–0.94	0.60	0.12	0.62**
Pregancy backfat thickness, mm	146	–15.61	8.07	2.45	0.01	–0.39	0.16	0.02	0.69
ADG 25 wk to pregnancy, kg	146	1.70	–0.16	0.22	0.48	0.002	0.014	0.91	0.60**
Daily backfat gain 25 wk to pregnancy, mm	146	–0.16	0.14	0.12	0.24	–0.012	0.008	0.14	0.43
Corpora lutea, no./gilt	146	4.19	2.75	1.29	0.04	–0.18	0.08	0.04	0.52**
Live embryos, no./gilt	146	4.99	1.67	2.08	0.43	–0.11	0.14	0.43	0.38
Live embryos at 30 d gestation/kg total feed	192	0.101	–0.015	0.010	0.12	0.0008	0.0006	0.23	0.40**
Independent variable: BW at 25 wk of age, start of breeding									
Dependent variable									
Day of breeding pubertal	162	–141.21	3.29	1.21	0.01	–0.016	0.006	0.02	0.34
Pubertal wt, kg	162	–67.87	2.94	0.90	0.01	–0.011	0.005	0.02	0.68**
Pubertal backfat thickness, mm	162	–44.84	1.18	0.30	0.01	–0.0049	0.0015	0.01	0.65**
ADG 25 wk to puberty, kg	162	3.04	–0.03	0.02	0.14	7.7E-05	1.1E-04	0.50	0.64**
Daily backfat gain 25 wk to puberty, mm	162	–0.28	0.02	0.01	0.29	–1.1E-04	7.6E-05	0.17	0.38
Day of breeding pregnant	146	–138.41	3.21	1.32	0.02	–0.015	0.007	0.03	0.40
Pregnancy wt, kg	146	8.96	1.38	1.22	0.27	–0.003	0.006	0.63	0.61**
Pregnancy backfat thickness, mm	146	–29.73	0.84	0.33	0.02	–0.003	0.002	0.09	0.66**
ADG 25 wk to pregnancy, kg	146	0.92	0.01	0.03	0.71	–1.4E-04	1.5E-04	0.35	0.61**
Daily backfat gain 25 wk to pregnancy, mm	146	–0.45	0.02	0.02	0.25	–1.2E-04	8.4E-05	0.16	0.41
Corpora lutea, no./gilt	146	–7.69	0.46	0.17	0.01	–0.0024	0.0009	0.01	0.53**
Live embryos, no./gilt	146	–2.65	0.28	0.28	0.31	–0.0014	0.0014	0.32	0.39
Live embryos at 30 d gestation/kg total feed	192	0.086	–0.0007	0.0012	0.57	1.3E-06	6.4E-06	0.85	0.40**
Independent variable: Day of breeding pubertal									
Dependent variable									
Pubertal wt, kg	162	93.67	0.78	0.24	0.01	–0.0002	0.0041	0.96	0.68**
Pubertal backfat thickness, mm	162	17.70	0.17	0.09	0.06	0.0003	0.0015	0.85	0.56**
ADG 25 wk to puberty, kg	162	0.50	0.013	0.008	0.09	–2.2E-04	1.3E-04	0.11	0.34
Daily backfat gain 25 wk to puberty, mm	162	0.28	–0.005	0.004	0.23	6.4E-05	7.1E-05	0.38	0.30
Day of breeding pregnant	146	1.47	0.98	0.10	0.01	–1.5E-05	1.8E-03	0.99	0.94**
Pregnancy wt, kg	146	93.81	0.91	0.31	0.01	–0.0035	0.0052	0.51	0.61**
Pregnancy backfat thickness, mm	146	17.31	0.16	0.09	0.09	0.0011	0.0015	0.47	0.62**
ADG 25 wk to pregnancy, kg	146	0.51	0.011	0.009	0.22	–1.7E-04	1.5E-04	0.26	0.43
Daily backfat gain 25 wk to pregnancy, mm	146	0.26	–0.004	0.004	0.36	5.6E-05	7.3E-05	0.45	0.34
CL, no./gilt	146	12.81	0.08	0.04	0.06	–6.4E-04	7.0E-04	0.37	0.56**
Live embryos, no./gilt	146	9.48	0.11	0.07	0.12	–0.0012	0.0012	0.31	0.41
Live embryos at 30 d gestation/kg total feed	162	0.039	–1.9E-06	3.4E-04	0.99	–3.9E-06	5.9E-06	0.51	0.33

[a]Model = Intercept + ($\beta 1$ * Independent variable) + ($\beta 2$ * {Independent variable}2) + litter.
[b]Intercept presented is intercept from regression analysis plus average of estimates for the random effect litter.
[c]Probability the estimate is not different than zero.
**$P < 0.01$.

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Table 5. Final model from step-down regression analysis for the dependent variable days to first estrus. Parameters were deleted sequentially using a minimal error-mean-square criterion

Parameter	Estimate	SE of estimate	*P*-value[a]
Intercept[b]	80.02	—	—
Daily GE intake during development period (dge)	1.32	14.31	0.93
25 wk wt, kg (25wkWt)	–0.92	1.66	0.59
25 wk backfat thickness, mm (25wkBF)	–32.56	10.37	0.01
ADG 25 wk to first estrus, kg/d (ADG_pub)	54.20	20.18	0.01
Daily gain in backfat thickness 25 wk to first estrus, mm/d (dgBF_pub)	–410.64	403.53	0.32
ADG_pub * ADG_pub	–13.49	5.76	0.03
dgBF_pub * dgBF_pub	–114.60	24.36	0.01
dge * 25wkBF	3.13	0.95	0.01
dge * dgBF_pub	186.65	151.94	0.23
25wkWt * 25wkBF	0.32	0.12	0.02
dge * 25wkWt * 25wkBF	–0.03	0.01	0.01
dge * 25wkWt * dgBF_pub	–1.14	0.96	0.24
dge * 25wkBF * ADG_pub	–0.17	0.10	0.11
dge * 25wkBF * dgBF_pub	–10.94	7.38	0.15
dge * 25wkWt * 25wkBF * dgBF_pub	–0.060	0.046	0.20
dge * 25wkWt * ADG_pub * dgBF_pub	–0.17	0.10	0.10
dge * 25wkWt * 25wkBF * ADG_pub * dgBF_pub	–0.009	0.005	0.10
$R^2 = 0.62$			

[a]Probability the estimate is not different than zero.
[b]Litter in which the gilts were born was included in the analysis and intercept adjusted for the influence of litter.

and backfat gains indicative of compensatory growth, and they exhibited first estrus sooner after entering the breeding facility than those that were heavier. Associated with compensatory growth are greater vital organ weights and fasting heat production (Koong et al., 1982), which are responses that may be favorable to reproductive development. The heaviest, fattest gilts, and the lightest, leanest gilts at the start of breeding exhibited first estrus sooner than those of the intermediate treatment groups. These findings suggest that the static measures of BW and backfat thickness are related to age at first estrus if above a threshold. In gilts that are below that threshold, the dynamic measures of rates of gain in BW and backfat thickness after entering the breeding facility influence the onset of first estrus; however, this may also be a threshold response.

Regression analyses indicated that daily GE intake during the 12-wk prepubertal development period, BW at the start of the breeding period, and day of the breeding period on which the gilts exhibited first estrus had significant influence on many of the traits considered to be important in reproductive performance of gilts. Development period GE intake and BW at the start of breeding were negatively related to ADG from the start of breeding to first detected estrus in this study, in which all gilts had ad libitum access to feed during the breeding period. Although gilts that were fed less GE during development, and thus were lighter in BW at the start of breeding, consumed greater quantities of feed during breeding and gained BW at a greater rate, the regression of pubertal day on development period GE intake was nonsignificant ($P > 0.05$). This regression result is in contrast to the hypothesis-testing results that indicated there was an effect ($P < 0.01$) of development period feed level on days to first estrus. Certainly, feeding the lower levels of GE during the development period followed by ad libitum access to feed during breeding did not delay onset of first estrus in these gilts.

Onset of first estrus may be one of the simpler, less complex reproductive responses measured. However, a step-down multiple regression analysis of day of first estrus on various independent variables indicates there are many interacting nonlinear determinants of day of first estrus (Table 5). The terms remaining in the model contribute to a reduction in the error mean square of the model; thus their inclusion improves the ability of the model to explain the dependent variable. The presence of interactions is evident in the treatment means presented in Table 3. Although ½Adlib gilts could have been considered deficient in BW and fatness at the start of the breeding period, they compensated for those deficiencies with greater rates of prepubertal BW and backfat gain during the breeding period. Conversely, the ⅞Adlib gilts had lower rates of prepubertal BW and backfat gain during the breeding period but had sufficient BW and fatness at the start of breeding to be able to exhibit first estrus in a timely manner, albeit later than the ½Adlib gilts, which demonstrated the greatest feed intake and gains during the breeding period. Those gilts that received the intermediate levels of dietary energy during

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the development were the latest to exhibit first estrus. Numerous workers have attempted to identify a single or a small number of static variables that would be predictive of day of first estrus (Rozeboom et al., 1995; Whittemore, 1996). This multiple regression model presents evidence that both static and dynamic variables may be determinants of the day of first estrus. Similar models, limited to the same independent variables, for other important reproductive traits (e.g., ovulation rate and number of live embryos) are equally or more complex and(or) account for less of the variation.

Efficiency of 30-d-old live embryo production may be the most relevant of the variables measured to determining the economic sustainability of pork production. There was an inverse relationship between GE intake during the development period and efficiency of 30-d live embryo production. This observation substantiates previous work by Klindt et al. (1999) that gilts that are fed less during the prepubertal development period are more efficient producers of 30-d-old embryos. Because feed accounts for approximately 60 to 70% of the inputs in a swine operation, a reduction in feed input must have a positive impact on the efficiency of the operation. Although efficiency of production of 30-d-old embryos is an important index, the truly important measure is efficiency of weaned pig production over the lifetime of the sow.

Some investigators recommend feeding developing gilts a 16% CP diet ad libitum until mating (Aherne and Williams, 1992; Boyd, 1999). Others recommend feeding for maximal rate of gain until a weight that approaches pubertal weight (~100 kg) and then moderately restricting feed until 10 to 14 d before the start of the breeding period, when gilts are to be offered an amount of feed that would induce a moderate flushing effect (Reese et al., 1995; NRC, 1998). Reese et al. (1995) recommends feeding gilts during the breeding period 3.0 kg/d. In a recent large evaluation of gilts, 2.75 kg of feed$\cdot$d$^{-1}\cdot$gilt^{-1} was fed during breeding that began at 180 d of age (NPPC, 2000). First estrus was detected at an average age of 220 d, or 40 d after start of the breeding period. That is considerably greater than the 15 to 28 d reported in this experiment. Published recommendations for feeding gilts during the breeding period may be less than what is required for minimal time to first detected estrus. The gilts provided near ad libitum access to feed during development (⅞Adlib) consumed greater than 3.0 kg/d during the breeding period. Limit feeding, even very moderate limit feeding, during breeding may compromise reproductive development.

Implications

Major determinants of economic sustainability of a swine operation are feed costs and the proportion of gilts that become pregnant and enter the sow herd. Nutritional management is the most manipulatable environmental factor that influences the efficiency with which gilts enter the sow herd. Gilts restricted to 50% of calculated ad libitum intake from 13 to 25 wk of age and provided ad libitum access to feed during breeding were the first to exhibit estrus and were the most efficient producers of embryos at 30 d of gestation. In contemporary, highly managed swine production systems, the use of managed nutritional strategies, periods of restriction, as well as periods of ad libitum access to feed, may allow improvements in the efficiency of pork production.

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