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Abstract

The preweaning litter environment of gilts can affect subsequent development. In a recent experiment designed to test the effects of diet on gilt development, litter-of-origin traits including individual birth weights, immunocrits (a measure of colostrum intake), sow parity, number weaned, and individual weaning weights were collected for approximately 1,200 gilts that were progeny of approximately 300 sows. Subsequently, BW, LM area, and backfat were measured at 100 d of age and at 28-d intervals until slaughter (260 d of age). From 160 d of age to slaughter, gilts were observed daily for estrus. At slaughter, the reproductive tract and 1 mammary gland were recovered. The reproductive tract was classified as cyclic or prepubertal; the number of corpora lutea was counted. Uterine horn lengths and ovarian dimensions were measured. Uterus and ovary samples from every 10th gilt were prepared for histological evaluation of uterine gland development and follicle counts, respectively. Mammary gland tissue protein and fat were assayed. Day of the estrous cycle at slaughter was calculated using the first day of the most recent standing estrus (d 0) recorded previous to slaughter. Each gilt development trait was analyzed for association with each litter-of-origin trait, after adjusting for dietary treatment effects. Uterine length, ovarian dimensions, mammary gland protein and fat, and uterine gland development were also adjusted for day of the estrous cycle at slaughter. All litter-of-origin traits were associated ($P < 0.05$) with growth traits. Top-down (backward elimination) multiple regression analysis indicated that BW and LM accretion in gilts was positively associated with immunocrit ($P < 0.01$), birth weight ($P < 0.01$), preweaning growth rate ($P < 0.01$), and parity ($P < 0.01$). Backfat accretion was positively associated with preweaning growth rate ($P < 0.01$), number weaned ($P < 0.05$), and parity ($P < 0.05$). Age at puberty was associated with birth weight (positive; $P < 0.01$) and preweaning growth rate (negative; $P < 0.01$). Total uterine length was positively associated with only birth weights ($P < 0.05$). Mammary gland protein was negatively associated with preweaning growth ($P < 0.01$). Mammary gland fat was positively associated with birth weight and number of piglets weaned ($P > 0.05$). These results indicate that colostrum consumption, birth weights, preweaning growth rate, number weaned, and parity are associated with gilt development traits during later life.

Keywords

follicle, growth, mammary, ovary, puberty, uterus

Disciplines

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Litter-of-origin trait effects on gilt development¹

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ABSTRACT: The preweaning litter environment of gilts can affect subsequent development. In a recent experiment designed to test the effects of diet on gilt development, litter-of-origin traits including individual birth weights, immunocrits (a measure of colostrum intake), sow parity, number weaned, and individual weaning weights were collected for approximately 1,200 gilts that were progeny of approximately 300 sows. Subsequently, BW, LM area, and backfat were measured at 100 d of age and at 28-d intervals until slaughter (260 d of age). From 160 d of age to slaughter, gilts were observed daily for estrus. At slaughter, the reproductive tract and 1 mammary gland were recovered. The reproductive tract was classified as cyclic or prepubertal; the number of corpora lutea was counted. Uterine horn lengths and ovarian dimensions were measured. Uterus and ovary samples from every 10th gilt were prepared for histological evaluation of uterine gland development and follicle counts, respectively. Mammary gland tissue protein and fat were assayed. Day of the estrous cycle at slaughter was calculated using the first day of the most recent standing estrus (d 0) recorded previous to slaughter. Each gilt development trait was analyzed for association with

each litter-of-origin trait, after adjusting for dietary treatment effects. Uterine length, ovarian dimensions, mammary gland protein and fat, and uterine gland development were also adjusted for day of the estrous cycle at slaughter. All litter-of-origin traits were associated ($P < 0.05$) with growth traits. Top-down (backward elimination) multiple regression analysis indicated that BW and LM accretion in gilts was positively associated with immunocrit ($P < 0.01$), birth weight ($P < 0.01$), preweaning growth rate ($P < 0.01$), and parity ($P < 0.01$). Backfat accretion was positively associated with preweaning growth rate ($P < 0.01$), number weaned ($P < 0.05$), and parity ($P < 0.05$). Age at puberty was associated with birth weight (positive; $P < 0.01$) and preweaning growth rate (negative; $P < 0.01$). Total uterine length was positively associated with only birth weights ($P < 0.05$). Mammary gland protein was negatively associated with preweaning growth ($P < 0.01$). Mammary gland fat was positively associated with birth weight and number of piglets weaned ($P > 0.05$). These results indicate that colostrum consumption, birth weights, preweaning growth rate, number weaned, and parity are associated with gilt development traits during later life.

Key words: follicle, growth, mammary, ovary, puberty, uterus

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INTRODUCTION

There has been a great deal of interest in characteristics of gilts that could be measured or manipulated early in their lifetime that might influence one or more production-related factors in later life. A recent study (Flowers, 2009) indicated that gilts raised in small litters compared with large litters reached puberty earlier and had subsequent improvement in retention in the breeding herd to later parities. Combined, this resulted in improvements in the number of pigs weaned per sow. Another recent report (Vallet et al., 2015) indicated that colostrum availability to neonatal piglets was negatively related to age at puberty and positively related to litter size. This is consistent with previous reports that colostrum availability increases neonatal uterine gland development (Chen et al., 2011; Bartol et al., 2013). These experiments suggest that key components of the litter environment in which gilts are raised influence subsequent performance and reproductive competence. During a recent effort to examine dietary influences on gilt growth, age at puberty and reproductive tract and mammary gland characteristics of commercial maternal line F_1 gilts (Calderón Díaz et al., 2015a,b), litter-of-origin data were collected on each gilt, which afforded an opportunity to examine relationships between preweaning traits and subsequent gilt development traits. Therefore, the objective of this study was to examine relationships between litter-of-origin traits (d 1 immunoglobulin immunocrit ratio [a measure of colostrum acquisition], birth weight, birth parity, preweaning growth rate, and number weaned in the litter) and growth and reproductive traits (BW, LM area, backfat, age and incidence of puberty, uterine length, ovulation rate, uterine gland development, ovary length and weight, number of ovarian follicles, and mammary gland fat and protein composition).

MATERIALS AND METHODS

Procedures involving animals were approved by the U. S. Meat Animal Research Center Animal Care and Use Committee and were consistent with Federation of Animal Science Societies (2010) guidelines. Three hundred three commercial maternal line sows were mated by AI using pooled commercial maternal line boar semen, and the resulting maternal line F_1 gilts were born in Smithfield Hog Production Division facilities (Circle 4 Farms, Milford, UT). Gilts were weighed at d 1 of age and uniquely identified with an ear tag, and a blood sample (2 mL) was collected and allowed to clot for 30 min. Serum was collected by centrifugation (1000 \times g for 10 min) and was then measured for immunoglobulin using the immunoglobulin immunocrit assay (Vallet et al., 2013). Parity and the total number of piglets born

and born alive were recorded. Normal cross-fostering of piglets was allowed within the first 48 h after birth to target a litter size during lactation of 10 to 13 piglets. When possible, males were cross-fostered and gilts remained with the birth sow. At weaning, age and BW of each gilt was recorded, and gilts were then transported to the site of the experiment (Smithfield Hog Production Division, Goldfield, IA).

Approximately 1,200 weaned gilts were distributed among 72 pens, with 36 pens in each of 2 barns. A full description of gilt housing, the dietary treatments that were applied, and the collection of traits at slaughter has been previously reported (Calderón Díaz et al., 2015a,b). Briefly, gilts were provided Smithfield standard grower diets to d 100 of age. At 100 d of age, gilts were weighed and backfat and LM area were measured by a trained technician using ultrasound (Biotronics, Ames, IA). At d 100 of age, gilts were randomly reassigned to pens and pens were randomly allocated to 6 different grower diets in a 3×2 factorial arrangement, with 3 levels of ME (high, medium, or low) and 2 levels of standard ileal digestible Lys (high or low). Gilts were fed treatment grower diets until they reached 90 kg BW and were then provided treatment finisher diets in the same factorial arrangement. At 28-d intervals, gilts were weighed and backfat and LM area were measured using ultrasound. Beginning at 160 d of age, gilts were exposed to vasectomized mature boars by placing boars directly in the pens and observed for behavioral estrus for 10 min daily. Individual boars were used on no more than 4 pens daily and were rotated among pens so that boars were not used on the same pens on consecutive days. Ten boars were used. Each individual date of standing estrus was recorded. Daily boar exposure continued until 3 d before slaughter at approximately 260 d of age. Gilts were slaughtered at a commercial processing plant (Natural Foods, Sioux Center, IA). One-third of the gilts were slaughtered on consecutive Wednesdays over a 15 day period. At slaughter, the reproductive tract and 1 mammary gland were collected from each gilt. For each gilt, 1 mammary gland directly below the rib cage was chosen for collection, to minimize damage to the belly. The mammary gland was excised from the body wall to include the skin and muscle wall. A block of mammary gland tissue was dissected from this sample to include all tissues from skin to muscle but excluding skin and muscle; therefore, the depth of the block was variable. One approximately 2-cm edge of the block was parallel to the midline, and the center of the edge began directly below the teat. The other 2-cm edge of the block was perpendicular to the midline and extended away from the midline. This resulted in a block of tissue approximately 2 by 2 cm by width of body wall from skin to muscle. Mammary gland fat (ether extract) and protein

(protein nitrogen) were measured in collected tissue samples using proximate analysis (Ward Laboratories, Kearney, NE). The length of each uterine horn and the width and height of each ovary were recorded for each gilt. The number of corpora lutea or corpora hemorrhagica was counted if present. Samples of the uterus and ovary from every 10th gilt on the slaughter line were placed into buffered formalin, embedded in paraffin, and processed for histological evaluation.

To evaluate uterine gland development, 2 hematoxylin- and eosin-stained uterine wall sections (10 μm) were examined. For each section, an area of the endometrium from lumen to myometrium was measured using computer-assisted morphometry (Bioquant, Nashville, TN). Then, the total area of glands within the endometrial area was measured by encircling each gland within the previously outlined endometrial area. Gland development for that section was then expressed as the ratio of gland area to endometrial area.

For ovaries prepared for histological evaluation, an approximately 5-mm-thick portion was cut from the center of ovaries and placed in a Mega-Cassette (Tissue-Tek, catalog number 4173; Sakura Finetek USA Inc., Torrance, CA) and fixed overnight in 10% neutral buffered formalin. The ovarian tissues were then postfixed and embedded in paraffin. Tissues were sectioned at 6 μm . A minimum of 10 sections were discarded between each section placed onto a slide to ensure that primordial, primary, and secondary follicles were not counted twice. Sections were stained with hematoxylin and counterstained with eosin. Three sections were evaluated for each gilt and preantral follicles were counted only in the section in which the nucleus of the oocyte appeared. Follicles were classified as described previously (Lents et al., 2014). Briefly, a primordial follicle consisted of an oocyte surrounded by a single layer of squamous pregranulosa cells, a primary follicle consisted of an oocyte surrounded by a single layer of cuboidal granulosa cells, a secondary follicle consisted of an oocyte surrounded by 2 or more layers of granulosa cells, and a tertiary/antral follicle consisted of an oocyte surrounded by 2 or more layers of granulosa cells with a distinct fluid-filled antrum.

Statistical Analysis

Prewaning growth rate of gilts was calculated by subtracting d 1 (birth) weights from weaning weights and dividing by the age at weaning. Right and left uterine horn lengths were summed to obtain the total uterine horn length for each gilt. Right and left ovarian widths and heights were averaged to obtain the average ovarian width and height. Daily detection of estrus allowed for the calculation of the day of the estrous cycle at slaugh-

ter for most gilts. Gilts that were prepubertal at slaughter were assigned -1 as the day of the estrous cycle during subsequent analyses, and gilts that were cycling at slaughter but did not have a prior observed estrus within 23 d before slaughter were deleted from the analysis. These gilts were assumed to be behaviorally anestrous. The linear and quadratic effects of day of the estrous cycle were included as covariates in analyses for uterine, ovarian, and mammary gland measures. The linear and quadratic effects of each litter-of-origin trait (immunocrit, birth weight, birth parity, preweaning growth rate, and number weaned) on each adult trait was analyzed by regression analysis using PROC GLM (SAS Inst. Inc., Cary, NC) after adjusting each adult trait for barn and dietary effects (ME, Lys, and ME \times Lys) and pen within barn \times ME \times Lys. For growth traits (BW, backfat, and LM area), the regression model also included linear and quadratic effects of day of age when measurements were taken. Uterine length, endometrial gland development, ovarian width and height, and mammary gland fat and protein analyses also included the linear and quadratic effects of day of the cycle. Because many litter-of-origin traits were correlated with each other, top-down (backward elimination) multiple regression analysis was used to provide a model that included all litter-of-origin traits that accounted for a significant independent fraction of the variance for each growth trait. The initial model included the linear and quadratic effects of all 5 litter-of-origin traits tested against each adult trait, and the nonsignificant litter-of-origin factor accounting for the least sum of squares in the model was iteratively deleted until a model was obtained that included all remaining significant litter-of-origin traits.

RESULTS

Growth Traits

Diet effects on adult traits were few and were previously reported (Calderón Díaz et al., 2015a,b). Table 1 summarizes the number of observations, means, SD, minimums, and maximums for the litter-of-origin and adult traits measured in this experiment. Individually, all litter-of-origin traits were significantly related to each growth trait, except immunocrit with LM area, but varied in the amount of variance explained by each trait. Resulting r^2 (proportion of variance) of each growth trait (BW, backfat, and LM area) explained by each litter-of-origin trait, as well as the linear and quadratic slopes of relationships and the final multiple regression model for each adult growth trait, are presented in Table 2. The greatest r^2 for BW and LM area was for relationships with birth weight. The greatest r^2 for backfat was the relationship with preweaning growth rate. To help

Table 1. Number of observations, means, SD, minima, and maxima for litter-of-origin and adult traits for gilts in this experiment

Trait	n	Mean	σ	Minimum	Maximum
Immunocrit	1,034	0.143	0.035	0.007	0.232
Birth (d 1) weight, kg	1,054	1.46	0.30	0.70	3.00
Prewaning growth rate, ¹ kg/d	1,000	0.23	0.06	0.04	0.49
Parity	1,052	4.2	1.8	2	8
Number weaned	1,000	9.2	2.1	1	14
BW, kg					
d 100	1,221	55.3	7.2	28.6	76.8
d 128	1,202	84.9	9.2	51.8	114.1
d 156	1,188	112.0	10.0	75.5	137.3
d 184	1,171	139.8	11.6	96.8	173.6
d 212	1,143	161.9	12.6	118.2	199.1
d 240	1,101	177.6	14.0	131.6	227.3
Backfat, cm					
d 100	1,016	0.87	0.16	0.38	1.50
d 128	1,002	1.11	0.22	0.51	2.06
d 156	990	1.46	0.32	0.58	2.82
d 184	975	1.96	0.44	0.76	4.17
d 212	951	2.62	0.60	1.09	5.00
d 240	934	3.17	0.74	1.24	6.32
LM area, cm ²					
d 100	1,016	19.8	3.0	10.7	27.7
d 128	1,002	29.7	4.0	16.1	44.4
d 156	990	36.8	4.3	24.1	51.9
d 184	975	42.8	4.5	29.7	61.0
d 212	951	47.7	4.8	34.5	68.8
d 240	934	51.5	5.3	37.4	71.3
Age at puberty	1,010	193.9	19.5	160	265
Ovulation rate	827	18.3	3.3	3	38
Total uterine length	968	298.3	84.3	74	555
Ovarian width	1,062	17.9	4.5	1.9	29.3
Ovarian length	1,063	26.7	5.3	7.9	45.1
Mammary gland fat, ² %	948	54.1	12.6	11.7	85.2
Mammary gland protein, ² %	948	8.6	2.7	2.8	17.3
Uterine gland area, ³ %	107	11.3	4.8	3.6	26.8
Number of follicles ⁴					
Primordial	107	40.0	27.0	5.7	149.7
Primary	107	4.3	2.7	.67	17.0
Secondary	107	3.9	2.5	.67	13.0
Antral	107	10.4	6.0	1.3	29

¹Prewaning growth rate calculated as weaning weight minus birth weight divided by weaning age.

²Mammary gland fat and protein are the result of proximate analysis and are on a DM basis.

³Uterine gland area is the percent of the endometrial area made up of uterine glands.

⁴Each individual observation is the mean of 3 different slides.

illustrate the relationships, the net increase or decrease in the growth traits that is associated with each litter-of-origin trait over its observed range of values is presented in Table 3. For BW, increases in all litter-of-origin traits were associated with increased BW values, except for parity, for which increased parity of birth was associ-

ated with decreased BW values. Positive associations between litter-of-origin traits and backfat were also found, except for a negative relationship between number weaned in the litter and backfat. For LM area, there was no relationship with immunocrit, and most of the other litter-of-origin effects were positive, except for parity. Similar to parity effects on BW, the relationship between parity and LM area was negative.

Top-down multiple regression analysis of BW resulted in a model that included the linear ($P < 0.01$) effect of immunocrit, linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of birth weight, linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of preweaning growth rate, and linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of parity. However, the addition of other litter-of-origin traits to the effect of birth weight alone accounted for only a further 4.7% (compared with 17.5% with birth weight alone) of the variation in adult BW. Multiple regression of adult LM area resulted in a model that included linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of immunocrit, linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of birth weight, the linear ($P < 0.01$) effect of preweaning growth rate, linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of parity, and the linear ($P < 0.05$) effect of number weaned. Similar to growth in BW, the addition of the other litter-of-origin traits to birth weight effects accounted for only an additional 2.3% of variation in LM area, versus 6.2% for birth weight alone. For both BW and LM area, the largest secondary contributor to the variance was preweaning growth rate. Finally, for backfat, the largest single contributor to the variance in backfat was preweaning growth rate. Multiple regression analysis resulted in a model that included the linear ($P < 0.01$) effect of immunocrit, the linear ($P < 0.05$) effect of birth weight, linear ($P < 0.01$) and quadratic ($P < 0.01$) effects of preweaning growth rate, the linear ($P < 0.05$) effect of parity, and the linear ($P < 0.01$) effect of number weaned. The number weaned effect was the second largest contributor to the variance in backfat in the multiple regression analysis. Multiple regression analysis of litter-of-origin effects on backfat provided an additional 1.1% of the variance compared with 1.5% contributed by preweaning growth rate alone. For the linear effect of parity, gilts from eighth-parity sows were fatter than gilts from earlier parities, but the number of gilts from eighth-parity sows in this experiment was limited. The increase in each growth trait calculated from the multiple regression that would result from optimizing each litter-of-origin trait is presented in Table 3.

Reproductive Traits

Preliminary analyses of uterine length, uterine gland measures, ovarian length and weight, and

Table 2. Percent of variance (r^2) of growth traits explained by the linear and quadratic effects (slopes in parentheses) of age of the gilt and each litter-of-origin trait individually and for all statistically significant linear and quadratic effects of litter-of-origin traits included in a multiple regression model

Litter-of-origin trait	BW	Backfat	LM area
Age	94.1 (1.42**, -0.0016**)	77.1 (-0.0046**, 0.000066**)	86.6 (0.47**, -0.00075**)
Immunocrit ¹	1.2 (81.26**, -179.06*)	0.81 (1.19**, NS ²)	NS (NS, NS)
Birth weight	17.5 (33.1**, -6.0**)	0.41 (0.098**, NS)	6.2 (12.4**, -3.0**)
Prewaning growth rate	9.9 (131.0**, -149.9**)	1.5 (3.2**, -4.97**)	1.9 (10.8**, NS)
Parity	0.74 (-0.54**, NS)	0.15 (0.01**, NS)	1.3 (-1.34**, 0.13**)
Number weaned	0.42 (1.41**, -0.07**)	0.44 (0.019**, -0.0019*)	0.29 (0.11**, NS)
All significant ³	22.2 ⁴	2.6 ⁵	8.5 ⁶

¹Linear and quadratic age effects accounted for a large portion of the variance of all 3 growth traits. The remaining litter-of-origin trait analyses were corrected for diet and age effects. The reported r^2 is the percent of variance accounted for by each litter-of-origin trait of the growth trait that remained excluding the variance for diet and age.

²NS = not significant.

³All significant is the r^2 for multiple regression analysis including all statistically significant ($P \leq 0.05$) litter-of-origin traits.

⁴Includes linear (18.0; $P < 0.01$) effect of immunocrit, linear (25.0; $P < 0.01$) and quadratic (-4.2; $P < 0.01$) effects of birth weight, linear (120.4; $P < 0.01$) and quadratic (-175.8; $P < 0.01$) effects of preweaning growth rate, and linear (-2.42; $P < 0.01$) and quadratic (0.21; $P < 0.01$) effects of parity ($P < 0.01$).

⁵Includes linear (0.97; $P < 0.01$) effect of immunocrit, linear (0.05; $P < 0.05$) effect of birth weight, linear (3.4; $P < 0.01$) and quadratic (-5.6; $P < 0.01$) effects of preweaning growth rate, linear (0.008; $P < 0.05$) effect of parity, and linear (-0.015; $P < 0.01$) effect of number weaned.

⁶Includes linear (-24.5; $P < 0.01$) and quadratic (89.1; $P < 0.01$) effects of immunocrit, linear (10.6; $P < 0.01$) and quadratic (-2.5; $P < 0.01$) effects of birth weight, linear (6.6; $P < 0.01$) effect of preweaning growth rate, linear (-1.5; $P < 0.01$) and quadratic (0.15; $P < 0.01$) effects of parity, and linear (0.06; $P < 0.05$) effect of number weaned.

* $P < 0.05$; ** $P < 0.01$.

mammary gland fat and protein indicated that each was affected by puberty and/or by the day of the estrous cycle when the gilts were slaughtered. The relationship between day of the estrous cycle and total uterine length is illustrated in Fig. 1. Puberty increased uterine length by approximately 100 cm (comparison of least squares means for gilts assigned -1 versus gilts assigned a true day of the estrous cycle). Total uterine length varied by another approximately 100 cm over the course of the estrous cycle. Because of this, the analyses of litter-of-origin effects on uterine length, uterine gland measures, ovarian length and weight, and mammary gland fat and protein were performed including the linear and quadratic effects of day of the estrous cycle as covariates.

In contrast to growth traits, reproductive traits were generally not as affected by litter-of-origin traits. Individual regression analysis of age at puberty, uterine length, ovulation rate, mammary gland protein, and ovarian length and width were not affected by immunocrit, the number weaned in the litter, or sow parity. Age at puberty was not associated with birth weight but was negatively ($P < 0.01$) associated with preweaning growth rate (linear slope = -241.9, quadratic slope = 465.9, $r^2 = 2.0\%$ after correction for dietary effects). Because the relationship was quadratic, it optimized at a preweaning growth rate of 0.26 kg/d, and the difference between age at puberty for the optimum versus the lowest value (0.04 kg/d) was a reduction in age at puberty of 22.5 d. Ovulation rate and ovary length and width were also not affected by birth weight or pre-

weaning growth rate. Uterine length was also not associated with preweaning growth rate but was positively associated ($P < 0.05$) with birth weight ($r^2 = 1.1\%$, linear slope = 22.1, difference in uterine length over the range of observed birth weights = 50.8 cm, after correction for diet and day of the estrous cycle at slaughter). Mammary gland protein was not associated with birth weight but was negatively ($P < 0.01$) associated with preweaning growth rate ($r^2 = 1.3\%$, linear slope = -5.5, difference across range of birth weights observed = -2.48%). Mammary gland fat was not associated with immunocrit, preweaning growth rate, or parity but was positively associated with birth weight (linear slope = 9.8; $P < 0.01$, and quadratic slope = -1.56; $P < 0.01$) and with the number of piglets weaned ($r^2 = 0.5\%$, linear slope = 0.42; $P < 0.05$). Mammary gland fat percent increased 9.3% over the range of birth weights observed (0.7 to 3 kg) and 5.5% over the range of number of piglets weaned (1 to 14). Primordial, primary, secondary, and antral follicle numbers in the ovary were not influenced by immunocrit, birth weight, preweaning growth rate, or parity. The number of antral follicles was negatively ($r^2 = 13.6\%$, linear slope = -0.98; $P < 0.05$) related to the number weaned in the litter. There were trends for similar negative relationships between number weaned and primordial ($P = 0.06$) and primary ($P = 0.051$) follicles but not with secondary follicles ($P = 0.14$). The difference in antral follicles over the range of number weaned observed (1 to 14) was -12.7. Lastly, percent gland area within the endometrium was

Table 3. Net increase or decrease in BW, backfat, or LM area over the observed range of values for litter-of-origin traits using slopes from Table 2 is presented. All positive indicates the increase in the trait that would result from the positive influence of all litter-of-origin traits included after multiple regression analysis (see Table 2)

Litter-of-origin trait	Range	BW, kg	Backfat, cm	LM area, cm ²
Immunocrit	0.007 to 0.23	+8.4	+0.27	NS
Birth weight	0.70 to 3.0 kg	+25.1	+0.22	+3.0
Prewaning growth rate	0.04 to 0.49 kg/d	+23.2	+0.25	+4.9
Parity	2 to 8	-3.24	+0.06	-0.24
Number weaned	1 to 14	+4.7	-0.12	+1.43
All positive	-	+36.1 ¹	+0.77 ²	+7.6 ³

¹Subtracts the results from an immunocrit of 0.23, birth weight of 3.0, preweaning growth rate of 0.49, and parity 2 from the results from an immunocrit of 0.007, birth weight of 0.7, preweaning growth rate of 0.04, and parity 8 using slopes from multiple regression reported in Table 2.

²Subtracts the results from an immunocrit of 0.23, birth weight of 3.0, preweaning growth rate of 0.49, parity of 8 and number weaned of 1 from the results of an immunocrit of 0.007, birth weight of 0.7, preweaning growth rate of 0.04, parity of 2 and number weaned of 14 using slopes from multiple regression reported in Table 2.

³Subtracts the results from an immunocrit of 0.007 (in multiple regression the effect of immunocrit reversed its sign), birth weight of 3.0, preweaning growth rate of 0.49, parity of 2 and number weaned of 14 from the results of an immunocrit of 0.23, birth weight of 0.7, preweaning growth rate of 0.04, parity of 8 and number weaned of 1 using slopes from multiple regression reported in Table 2.

unaffected by immunocrit, birth weight, preweaning growth, parity, or number weaned as individual traits.

Top-down multiple regression analysis indicated no effects of litter-of-origin traits on ovulation rate and ovarian dimensions. Multiple regression of age at puberty resulted in a model including the linear effect of birth weight and the linear and quadratic effects of preweaning growth rate ($r^2 = 2.6\%$ after correction for dietary effects, linear slope birth weight = 6.4, linear slope preweaning growth rate = -232.6, quadratic slope preweaning growth rate = 421.7). A surface plot of this relationship is illustrated in Fig. 2. As with the effect of preweaning growth rate alone, the effect of preweaning growth was optimized at 0.28 kg/d. Therefore, the maximum difference one could expect from optimum birth and preweaning growth using the range of values available and the results of the multiple regression is a reduction of 38.1 d in age at puberty (comparing the results of 3 kg birth weight and 0.04 kg/d preweaning growth rate with the results of 0.7 kg birth weight and 0.28 kg/d preweaning growth). The surface plot (Fig. 2) indicates that the combined effects of high birth weight and slow preweaning growth predispose gilts to a later age at puberty.

Multiple regression of uterine length indicated that only birth weight significantly affected uterine length. Top-down multiple regression of mammary gland

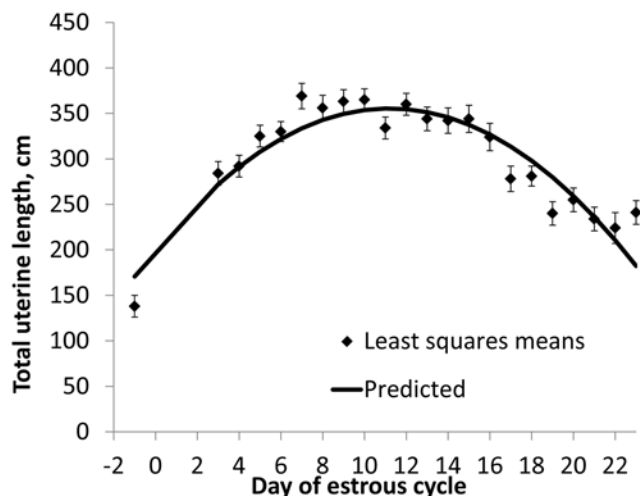


Figure 1. The relationship between day of the estrous cycle and total uterine length is illustrated. Individual points are least squares means \pm SE for uterine length for each day of the cycle. Number of observations for each least squares mean ranged from 28 to 69.

protein indicated that it was associated with only preweaning growth rate. Top-down multiple regression of mammary gland fat indicated significant associations with only number weaned in the litter-of-origin; the effect of birth weight on mammary gland fat dropped out of the analysis, even though the effect appeared to be larger when each was performed separately. Top-down multiple regression analysis of follicle numbers did not result in further relationships in addition to the effect of number weaned. Top-down multiple regression of percent gland area within the endometrium resulted in no relationships with litter-of-origin traits.

DISCUSSION

The number of quality pigs weaned by female swine in their lifetime in the breeding herd has been suggested to be an economically relevant measure of their reproductive competence (Serenius and Stalder, 2006). This measure takes into account many subordinate factors that contribute to the overall outcome, including growth; fat levels; achievement of puberty; successful mating and farrowing at each parity; litter size, preweaning mortality, and lactational competence within each litter; and problems of structural soundness that might influence premature culling (Serenius et al., 2006; Serenius and Stalder, 2007). Many of these factors may be influenced by developmental events that occur before weaning. Results of the current study indicate that litter-of-origin traits were associated with subsequent growth, age at puberty, uterine length, mammary fat and protein, and antral follicle number but not ovulation rate, endometrial gland, or primordial, primary, or secondary ovarian follicle number. Immunocrits, birth weight, preweaning growth rates, parity, and number weaned in

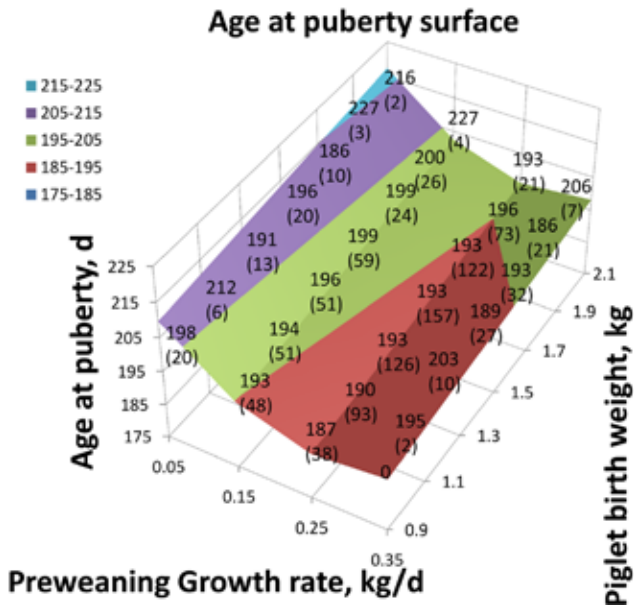


Figure 2. Surface plot illustrating the combined relationship between birth weight, preweaning growth rate, and age at puberty in gilts. Least squares means and number of observations are indicated for each birth weight and preweaning growth rate combination observed in this experiment. Effects of both birth weight and preweaning growth rate were statistically significant. The surface plot and least squares means both suggest that large birth weight piglets that do not grow well during lactation are associated with older age at puberty.

the litter were associated with changes in BW, backfat, and LM area. Curiously, in multiple regression analysis, preweaning growth was negatively related and birth weights were positively related to age at puberty, despite both being positively related to BW growth. Birth weights were positively associated with uterine length but did not influence uterine gland development, the size of the ovary, or the number of follicles. These results indicate that the litter environment influences some adult growth and reproductive characteristics but not others.

Multiple regression analysis implicated different rankings of litter-of-origin traits affecting BW and LM area growth compared with backfat growth. The litter-of-origin trait explaining the most variation in BW and LM area growth was birth weight, with the second being preweaning growth rate. By contrast, the most variation in backfat was explained by preweaning growth rate, the second most influential was access to colostrum (immunocrit), and birth weights were fourth behind number weaned. It seems possible that given these interrelationships, relative fat to lean body composition might be altered by differential emphasis on birth weights and preweaning growth rate, such that high birth weight piglets that gain weight slowly during the preweaning period would be expected to be leaner than similar size littermates that grow faster during the preweaning period.

The combined effects of birth weight and preweaning growth rate appear to affect age at puberty. Large

birth weight piglets that grow slowly were predisposed to a later age at puberty in this trial. This could be the result of subtle variations in body composition as the gilts grew, because reduced accumulation of fat has been reported to be associated with older age at puberty (Gaughan et al., 1997), although this effect is controversial (Rozeboom et al., 1995). On the other hand, rather than a causal effect of body fat on age at puberty, it is possible that puberty might have a causal effect on accumulation of fat (Kirkwood and Aherne, 1985). It seems possible that larger piglets at birth might be predisposed to mature at a later age, with slow preweaning growth further increasing the time to maturity. Once puberty is attained, gilts may begin to accumulate fat. Correlative relationships are difficult to discern cause and effect, and one goal of this experiment was to alter body composition by changing ME and Lys in the diets. Unfortunately, very little change in body composition occurred due to diet (Calderón Díaz et al., 2015b), and consequently, no differences in age at puberty occurred. Determining cause and effect of body composition and age at puberty will require further experiments. Nevertheless, the current data suggest that selection of gilts for the breeding herd that were heavy at birth and subsequently grew slowly during the preweaning period should be avoided if early puberty is the goal.

The negative relationship between preweaning growth rate and age at puberty in this experiment is entirely consistent with previous reports that gilts raised in a small litter experience earlier puberty (Flowers, 2009). Gilts raised in a small litter environment would be expected to grow faster during the preweaning period due to reduced competition among littermates for access to the mammary gland. Flowers (2009) further concluded that gilts raised in small litters had improved retention in the breeding herd, suggesting that preweaning growth rate might improve retention of gilts in the breeding herd. Age at puberty and retention in the breeding herd are known to be associated (Knauer et al., 2010). We cannot address the possibility that birth weights and preweaning growth rates affect herd retention with the data available from this experiment, but a subsequent trial is planned in which litter-of-origin data will be collected and sows will be monitored to third parity.

Previous results indicated a variety of relationships between the immunocrit and adult performance traits (Vallet et al., 2015). Previous reports indicate that immunocrits were positively associated with growth, litter size, and lactational performance and negatively associated with age at puberty (Vallet et al., 2015). This study confirms the positive relationship between growth rate and immunocrit, indicating that increased colostrum availability predisposes piglets to faster growth into adulthood. Multiple regression analysis of LM area and

backfat measures in this experiment suggested that colostrum availability contributed independently to both backfat and LM area growth, with some evidence of a greater influence of colostrum availability on backfat compared with LM area. The present experiment did not confirm a relationship with age at puberty, despite a clear relationship between the immunocrit and growth. In the present experiment, gilts were fed *ad libitum* throughout the trial. In the previous report, gilts were *ad libitum* fed until 170 d of age and were subsequently limit fed (Vallet et al., 2015). Limit feeding in the previous report may have placed more emphasis on feed efficiency among gilts, allowing the effect of the immunocrit on age at puberty to be detected. Because gilts are not typically limit fed during development, the importance of colostrum effects on age at puberty seems unlikely, given the results of the current experiment. Immunocrit relationships with age at puberty and litter size will be further tested in subsequent planned experiments.

Uterine length differed greatly between prepubertal and pubertal gilts and during the estrous cycle. The differences in uterine length before and after puberty are consistent with previous reports (Guo et al., 1998; Stancic et al., 2011), although the lengths measured in this study were greater than either previous report. Gilts used by Guo et al. (1998) were much younger and puberty was induced, which could explain the difference in length compared with the current report. Stancic et al. (2011) observed gilts at 7 mo of age, which would be an age similar to that in the current report, but they did not adjust observations for differences due to the estrous cycle. Differences observed in uterine length during the estrous cycle agrees with a previous report of uterine length measures during early pregnancy (Perry and Rowlands, 1962) but is not consistent with another report of uterine length measures during early pregnancy (Chen and Dziuk, 1993), where it was reported that uterine length does not vary from d 6 onward. The differences in uterine length during the cycle were not due to differences in contractility of the uterus during the cycle, because measures were made 24 h after slaughter when all contractility of the uterus had been lost. Therefore, future studies of differences in uterine length must take into account differences during the cycle, by either collecting tissues on the same day of the cycle or by fitting day of the cycle as a covariate.

Few relationships were obtained between litter-of-origin traits and uterine, ovarian, and mammary gland measures. Notable exceptions were a relationship between birth weights and uterine length and a relationship between the number of piglets weaned and the number of antral follicles. The relationship between birth weights and uterine length, with an estimated difference of approximately 50 cm over the range of birth weights ob-

served, suggests that there should be a relationship between birth weight and uterine capacity, perhaps being reflected in increased litter size in larger gilts at birth. To our knowledge, this possible relationship has never been explored. The relationship between number of piglets weaned and number of antral follicles seems large and is very curious, because the effect does not appear to be due to differences in birth weights or preweaning growth rates nor is it reflected in changes in ovulation rate. Behavioral interactions or differences in qualitative aspects of milk that might differ with the number of piglets nursed may influence later antral follicle development.

Mammary gland protein and fat were measured to obtain a crude assessment of gland development in gilts. Assessment of protein was intended to provide a possible measure of duct cellularity in the gland, whereas our assessment of fat was intended to provide a measure of the possible interference of fat cell development with mammary gland development. The negative influence of high nutrition on milk production in cattle is well known (Sejrsen and Purup, 1997) and may, in part, be explained by compositional changes in the developing mammary gland (Swanson, 1960; Capuco et al., 1995; Meyer et al., 2006). Specifically, greater fat in the mammary fat pad is associated with reduced production, but similar results indicating a correlation between gland composition and function in swine are not available. Nevertheless, positive relationships between mammary gland protein and preweaning growth and between mammary gland fat and birth weight and/or number weaned in the litter-of-origin were observed. Therefore, if high mammary gland protein and low fat are indicative of improved mammary gland function as suggested by results in cattle, one might suggest that greater preweaning growth would be associated with improved mammary gland development and therefore improved lactation. Greater birth weights or greater number weaned in the litter-of-origin promoted fat deposition in the mammary gland, which could interfere with development and reduce subsequent lactation performance. These possible effects will be tested in our future trial in which sows will be observed until third parity and lactation performance data will be collected.

Curiously, there was no relationship between the immunocrit and gland development within the uterus. Previous reports indicate that development of endometrial glands is delayed in piglets that receive milk replacer compared with those that receive colostrum (Chen et al., 2011; Miller et al., 2013; Bartol et al., 2013). In addition, previous reports indicated that immunocrit values on d 1 are associated with litter size in adult pigs (Vallet et al., 2015). These reports combined suggested that the delay in early gland development may have resulted in impaired gland development in adult gilts that received

reduced colostrum as measured by the immunocrit. However, current results indicate that the area of the endometrium made up of glands differs during the estrous cycle, with the greatest percentage being found during mid cycle (d 11). It was not possible to slaughter all gilts at the same stage of the cycle, and it is possible that correction of gland area for the stage of the cycle may be incomplete or incorrect. It is also possible that the number of gilts with low immunocrit that were examined was insufficient to demonstrate the true effect. There were only 3 gilts that had immunocrits below the 0.05 threshold that we have previously used to indicate that a piglet was colostrum deficient (Vallet et al., 2013). We are currently performing a follow-up experiment comparing colostrum-deficient piglets and their normal littermates with regard to both endometrial gland development and uterine protein secretion during early pregnancy.

In summary, our results indicate that litter-of-origin characteristics such as birth weight, colostrum acquisition (immunocrit), and preweaning growth rate affect the growth rate of gilts. Results further indicate that age at puberty is delayed for piglets with large birth weights that grow slowly during the preweaning period. Of the litter-of-origin traits measured, the single biggest predictor of growth of BW and LM area is birth weight followed by preweaning growth rate. By contrast, the single biggest litter-of-origin predictor of backfat deposition is preweaning growth rate followed by colostrum acquisition as measured by the immunocrit. Uterine length was related to birth weight but not to other litter-of-origin traits. Given these results, reduction in age at puberty might be accomplished by improvements in preweaning growth rates, ostensibly by raising gilts in smaller litters as suggested by Flowers (2009) or through improvements in milk production by sows.

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