# Duration of lactation, endocrine and metabolic state, and fertility of primiparous sows

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# Duration of lactation, endocrine and metabolic state, and fertility of primiparous sows[1,2]

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**ABSTRACT:** The objectives of this study were to determine factors affecting the reproductive performance of primiparous sows early weaned (EW; n = 35) at d 14 or conventionally weaned (CW; n = 35) at d 24 of lactation. Sow BW and backfat were recorded at farrowing, weekly until weaning, and at standing heat. Feed intake was controlled throughout lactation to standardize nutritional effects on subsequent reproductive performance. Litter size was standardized across treatments within 48 h after farrowing, and litter weight was recorded until weaning. In subsets of sows, blood samples were collected from 10 h before to 10 h after weaning, and then every 6 h until ovulation. Sows were heat checked twice daily and bred at 24-h intervals during standing heat using pooled semen. Ultrasonography every 6 h determined time of ovulation. Sows were either slaughtered within 24 h after ovulation to assess ovulation rate, fertilization rate, and embryonic development in vitro, or at d 28 of gestation to determine ovulation rate and embryonic survival. Compared with CW sows, EW sows had more backfat at weaning (15.9 ± 0.5 vs. 14.7 ± 0.5 mm; $P < 0.001$). Also, CW sows tended to lose more BW and to have lower IGF-I concentrations, indicating poorer body condition. Duration of lactation did not affect ovulation rate (EW = 17.6 ± 0.7; CW = 18.7 ± 0.6), fertilization rate (EW = 96.0 ± 2.2; CW = 88.2 ± 4.7%), or embryo survival to d 28 (EW = 62.5 ± 4.5; CW = 63.1 ± 5.0%). There was a marginal effect of duration of lactation on weaning-to-estrus interval (EW = 120 ± 3; CW = 112 ± 3 h; $P < 0.06$) and duration of estrus (EW = 52.4 ± 2.3; CW = 46.3 ± 2.2 h; $P < 0.08$). Overall, embryonic survival, not ovulation rate, seems to be the limiting factor for potential litter size in the second parity. Although fertility in both EW and CW sows studied was compromised, endocrine and metabolic data indicate that the mechanisms affecting reproductive performance may differ between the two weaning systems. The LH, FSH, and estradiol data from the EW sows are characteristic of animals with limited follicular development and incomplete recovery of the hypothalamic-pituitary-ovarian axis; consequently, the integrity of the uterine environment may be adversely affected and limit embryonic survival. In CW sows, variability in metabolic state seemed to be the key factor limiting the fertility, again adversely affecting embryonic survival.

Key Words: Endocrinology, Fertility, Lactation, Metabolism, Sows

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## Introduction

Decreased productivity of sows weaned at 14 d or less can be a source of economic loss for producers (Foxcroft, 1997). A proper understanding of the physiology of the sow before and after weaning is fundamental to understanding reproductive problems associated with early weaning. In previous studies, LH secretion was attenuated after early weaning (Edwards and Foxcroft, 1983a,b; Kirkwood et al., 1984), but similar data are lacking for early-weaned sows of contemporary commercial genotypes. Although early weaning is associated with a longer weaning-to-estrus interval, effects on duration of estrus and time of ovulation have not been investigated. Inconsistent effects of early weaning on embryonic survival have been reported (Marsteller

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et al., 1997; Belstra et al., 2002). When embryonic survival is adversely affected, it is not known whether the uterine environment or the competence of the developing embryo is primarily responsible. Early weaning may impact the uterine environment because of incomplete uterine involution (Foxcroft et al., 1995). With extended lactations, catabolism of body tissues in primiparous sows delays maturation of ovarian follicles (Yang et al., 2000a; Clowes et al., 2003) and the oocyte (Zak et al., 1997b; Yang et al., 2000a). Therefore, depending on the duration of lactation, fertility of weaned primiparous sows may be affected by different mechanisms.

A proper understanding of the cause of variable fertility in commercial dam-line sows with different duration of lactation is needed as the basis for optimizing management strategies. The objectives of this study were to define: 1) temporal relationships among endocrine changes before and after weaning, ovulation rate, and the timing of ovulation and insemination, 2) fertilization status and in vitro development of recovered oocytes, and 3) embryonic survival to d 28 of gestation, as key determinants of postweaning fertility in primiparous sows subjected to different durations of lactation.

## Materials and Methods

### *Animals, Treatments, and Feeding Regimen*

This research was performed in accordance with the Canadian Council on Animal Care guidelines and with the approval of the University Animal Policy and Welfare Committee. Within each of four replicates available for study between late July and November, primiparous $F_2$ sows (n = 70; Manor Hybrid × Large White; Genex Swine Group Inc., Regina, SK, Canada) were stratified across two treatments based on their weight and backfat depth measured 65 mm off of the midline at the 10th rib on d 109 of gestation. Day of farrowing was considered d 0. Early-weaned (**EW**; n = 35) sows were weaned on d 14 and conventionally weaned sows (**CW**; n = 35) on d 22 to 25 (mean = 23.7 ± 0.6) of lactation. In an attempt to remove effects of variable feed intake and metabolic state from the experimental model, sows of similar weight and backfat from each treatment were subjected to a pair-feeding regimen (see below). Additionally, litter size was standardized across treatment pairs by cross fostering within 48 h after farrowing. In the majority of sows, litter size was standardized to either 9 (16 pairs) or 10 (13 pairs) piglets; one pair of sows suckled 7, 8, and 12 pigs, respectively, and three pairs of sows suckled 11 pigs. Litter processing was performed within 24 h after farrowing using standard protocols.

Sows were fed a standard lactation diet (18% CP, 3,400 MJ of energy) using a step-up feeding regimen and pair feeding in an attempt to regulate feed intake and body condition. Fresh feed was offered at 0800, 1200, and 1500; at 1600, feed was removed and weigh-backs were performed to determine feed disappearance. Sows were offered 2.5 kg of feed on the day of farrowing and subject to zero weigh-back in both sows in a pair, feed was increased by 0.5 kg/d until d 14. However, from the day after farrowing until d 14, both pair-fed sows were offered the lowest quantity of feed consumed by either sow the previous day. When one sow in a designated pair farrowed later than the other, feed for the first sow to farrow was increased more gradually until the second sow had farrowed, after which pair feeding commenced. After weaning the EW group (and again, subject to zero weigh-backs), feed offered to pair-matched CW sows increased every other day by 0.5 kg/d until weaning on d 24. Sows and piglets had ad libitum access to water throughout the experimental period. Creep feed was not available to piglets during lactation.

From weaning until the onset of standing heat, sows were offered 1.8× maintenance requirements based on weaning weight. Sows were fed twice daily (morning and afternoon) and daily weigh-backs were performed to estimate daily feed intake. At the onset of standing heat, feed was reduced to NRC requirements for gestating sows (1.5× maintenance) until slaughter.

Sow BW and backfat and litter weights were determined within 24 h of farrowing (d 0), at weekly intervals during lactation (EW = d 7; CW = d 7, 14, 21), and at weaning (EW = d 14; CW = d 22 to 25). Litter weights were also determined any time litter size changed. Sow BW and backfat were measured again at the onset of standing heat and the day of transport to the abattoir.

### *Blood Sampling for Hormone Assessment*

Between d 2 and 5 of lactation, approximately one half the sow pairs (n = 17 CW; n = 17 EW) underwent surgery for the insertion of an indwelling jugular catheter via the cephalic vein. An intensive (4 mL; 15-min interval) 20-h sampling (0000 to 2000) was completed from 10 h before until 10 h after weaning at 1000 on d 14 or 24. At the time of weaning, piglets were removed from the sows and the number of piglets and litter weights recorded. Sows remained in the farrowing crate overnight and were moved to the breeding barn early the next day. Starting at 0000 on the day after weaning (4 h after the last intensive sample was taken), 8-mL blood samples were collected at 6-h intervals until ovulation occurred. Plasma samples collected during the intensive bleed were analyzed for LH, FSH, and IGF-I. Samples taken at 6-h intervals after weaning were analyzed for estradiol, LH, FSH, and IGF-I. Based on published data indicating that differences in plasma progesterone in the immediate postovulatory period are associated with differences in early embryonic survival (see Zak et al., 1997a; van den Brand et al., 2000), a 3-mL blood sample was obtained from an ear vein in noncannulated animals, and via the cannula in cannulated sows, 24 h after ovulation for the determination of plasma progesterone concentration. Cannulae were removed after taking the last sample.

*Management After Weaning*

After weaning, cannulated sows were housed individually and noncannulated sows were group housed. Estrus detection was performed twice daily for 15-min periods at 0600 and 1800 using backpressure testing by an experienced technician, having moved sows to the same test arena that allowed good fenceline contact with three mature vasectomized boars. From the onset of standing heat, a combination of transcutaneous and transrectal ultrasonography with a 5.0 to 7.5-MHz multiple angle transducer (Pie Medical Scanner 200, model 41480, Can Medical, Kingston, ON, Canada) at 6-h intervals was used to monitor ovarian follicular development. Time of ovulation was determined as the time of the first ultrasound scan when no preovulatory follicles were observed. Sows were classified as anestrous if they had not exhibited estrus by d 10 postweaning (weaning = d 0).

All estrous sows (32 EW and 33 CW) were artificially inseminated at detection of standing heat and every 24 h until ovulation using pooled semen ($3 \times 10^9$ spermatozoa/dose) from the same group of three boars designated for use throughout this experiment (Alberta Swine Genetics Corp., Leduc, AB, Canada). For study of embryonic development in vitro, a total of 27 sows were slaughtered 6 to 24 h after ovulation either at a local abattoir (animals in Replicates 1 to 3 that ovulated on Sunday and Tuesday evenings; n = 15 EW; n = 8 CW) or at the research unit (all sows in Replicate 4: n = 2 EW; n = 2 CW). Remaining sows (n = 15 EW; n = 23 CW) were slaughtered at the local abattoir on d 25 to 37 of gestation to determine embryonic survival.

*Assessment of Embryonic Survival In Vivo*

Immediately after slaughter, reproductive tracts were recovered and transported to the laboratory. Ovulation rate, embryonic survival rate (**ESR**) based on the number of viable embryos, embryonic crown to rump length measured within the amnion, and allanto-chorionic fluid volume as a measure of placental size were determined using established procedures (Almeida et al., 2000).

*In Vitro Assessment of Embryonic Development*

For sows slaughtered 6 to 24 h after ovulation, reproductive tracts were recovered, transported at 39°C to the laboratory, and ovulation rate was recorded. Recovery and culture of fertilized oocytes was then carried out as described previously (Novak et al., 2003). Briefly, embryos recovered at the one- to two-cell stage were incubated under sterile conditions in controlled media and incubation conditions. The proportion of embryos proceeding to the morula and blastocyst stage of development within 144 h was scored as a measure of embryonic development in vitro. As embryos collected at later stages of development are more likely to become morulae or blastocysts, data from sows with oocytes beyond the two-cell stage at recovery were omitted from this analysis.

*Hormone Assays*

Plasma LH and FSH concentrations were determined in duplicate using the homologous double antibody RIA previously described by De Rensis et al. (1991) and Hunter et al. (1993), respectively. For LH, 200 μL of plasma was assayed, the intra- and interassay CV were 8.29 and 8.70%, respectively, and the sensitivity of the assay was 0.07 ng/mL. For FSH, 300 μL of plasma was assayed, the intra- and interassay CV were 9.46 and 8.91%, respectively, and the sensitivity of the assay was 14.11 ng/mL. Plasma IGF-I concentrations were determined in duplicate using a homologous double antibody RIA as described by Cosgrove et al. (1992), with modification to the antiserum as described by Novak et al. (2003). One hundred microliters of plasma was initially extracted with 3 mL of acid ethanol. Radio inert recovery efficiency was 112.4%. The intra- and interassay CV were 11.3 and 12.1%, respectively, and the sensitivity of the assay was 24.30 ng/mL. For determination of plasma estradiol concentrations, 1 mL of plasma was extracted by the addition of 5 mL of diethyl ether and vortexed for eight 1-min pulses. Plasma samples taken immediately before and at the time of the LH surge were diluted 2.5-fold with assay buffer before extraction. Extraction efficiency was 67.8%, and sample potencies were not corrected for recovery. Estradiol concentrations were then determined in duplicate samples of extract using a double antibody RIA kit from Diagnostic Products Corp. (Los Angeles, CA) previously validated for use with porcine plasma (Yang et al., 2000b). The intra- and interassay CV for the assay were 6.40 and 8.07%, respectively, and sensitivity of the assay was 1.20 pg/mL. Plasma progesterone concentrations were determined in duplicate using an established RIA (Coat-A-Count progesterone; Diagnostic Products) previously validated for use with porcine plasma without extraction (Mao and Foxcroft, 1998). The intraassay CV for the single assay run was 8.68%, and the sensitivity of the assay was 0.11 ng/mL.

*Statistics*

Prediction equations developed by Clowes (2001) for the same genotype as that in the present experiment, and modified from Whittemore and Yang (1989), were used to estimate body muscle mass (muscle mass, kg = –4.84 + 0.394 BW – 0.633 BF) and fat mass (fat mass, kg = –7.75 + [0.078 BW + 0.762 BF]) during lactation and after weaning, where BW = sow live weight (kg) and BF = sow backfat.

Sow energy balance during lactation (lact) and after weaning (wean) were determined according to the formula of Noblet et al. (1990) and converted to Mcal ME/d:

$$EB_{lact} = [FI \times ED - (22.0 \times BW + 6.83 \times LG - 125 \times n + 1{,}430)]/1{,}000$$

where $EB_{lact}$ = energy balance (Mcal of ME/d); FI = feed intake (kg); ED = energy density in the feed (kcal of ME/kg); BW = mean sow body weight over the period (kg); LG = body weight gain of the litter over the period (g/d); and n = the number of pigs in the litter. Energy balance after weaning was calculated as follows:

$$EB_{wean} = FI \times ED - 110 \times BW^{0.75}$$

where $EB_{wean}$ = energy balance (Mcal of ME/d); FI = feed intake (kg); ED = energy density in the feed (kcal of ME/kg); and BW = mean sow body weight over the period (kg).

Data were analyzed as an incomplete randomized block design using only data from 33 sow pairs that completed the full experimental protocol. Treatment effects on litter growth rate, feed intake, BW and backfat changes and energy balances during lactation and postweaning, ovulation rate, weaning-to-estrus interval (h), interval from last insemination to ovulation, estrus duration, time of ovulation in relation to onset of estrus, number and crown to rump length of embryos, allantoic volume, and ESR at d 28 (arcsin transformed data) were analyzed using the GLM procedures of SAS (SAS Inst., Inc., Cary, NC). The complete model included replicate and treatment as the main effects, sow as the experimental unit, and the sow within treatment × block interaction as the error term. The analysis of BW and backfat at weaning included BW and backfat at d 7 as covariates. The analysis of BW and backfat during the postweaning interval used the previous measure of BW and backfat as covariates (for example, in the analysis of standing heat backfat, backfat at weaning was used as a covariate). Analysis of embryo crown to rump measurement and allantoic volume used the day of slaughter as a covariate. In the event that significant treatment effects were established, multiple comparisons were performed using the Student-Neuman-Keuls test. Evaluation of treatment effects on ovulation rate, oocyte recovery rate, fertilization rate, and embryo developmental competence in vitro was performed by the GLM procedure of SAS after log- or arcine-transformation of data to achieve normal distributions of variance as appropriate.

For the intensive 20-h period of sampling before and after weaning, plasma LH data were analyzed as mean concentrations over successive 5-h periods, and as mean LH pulse frequency over the 10-h periods before and after weaning. An LH pulse was defined as an increase from baseline to peak within one sampling interval, followed by a logarithmic decay in LH concentrations involving four samples between the peak and nadir in LH, as described by Shaw and Foxcroft (1985). Hourly estimates of plasma FSH and IGF-I concentrations over the 10-h periods before and after weaning were used to establish immediate responses to weaning. Longer-term responses to weaning were analyzed using 6-hourly period samples for estradiol, LH, FSH, and IGF-I over the 72-h period starting at 0000 on d 1 after weaning. Endocrine changes over the periestrous period were analyzed after normalizing LH, FSH, and estradiol data to the peak of the LH surge (time zero), using 6-hourly period samples from 72 h before until 24 h after the peak of the LH surge. Treatment effects over time for all these endocrine variables were analyzed by the repeat-measures ANOVA procedures of SAS; the model included treatment, time and replicate as the main effects. To compare the magnitude of the proestrous rise in plasma estradiol and the magnitude of the preovulatory LH and FSH surges, endocrine profiles after weaning were visually appraised to determine the preovulatory surge peak values of each hormone and to establish appropriate criteria to estimate total hormone secreted during the surge period. With the peak LH concentration set as time zero, three samples before and four samples after this zero point were included in the estimate of total LH secretion during this surge period. With the peak FSH concentration set as time zero, one sample before and two samples after this zero point were used to estimate total concentrations during the FSH surge. Finally, with the peak estradiol concentration set as the zero point, six samples before and four samples after this zero point were used to estimate total concentrations during the estradiol surge. The sum of the individual concentrations for each time point included was then used as an estimate of total hormone released during the estradiol, LH, and FSH surges for each sow. The intervals between peak LH, FSH, and estradiol concentrations, and estimates of total surge release of hormones, were then analyzed by the GLM procedure of SAS. In the event that significant treatment effects were established, multiple comparisons were performed using the Student-Neuman-Keuls test. All data are presented as means ± SEM.

Chi squared analysis (SAS, PROC FREQ) was used to determine differences between the number of anestrous and open sows, number of breedings, age of semen, and overall failure to rebreed between treatment groups. Correlation analysis (SAS, PROC REG) was used to examine associations between feed intake, endocrine, metabolic, and various reproductive parameters.

## Results

### *Litter Characteristics*

Of the 35 sows initially designated for pair feeding in each treatment, two CW sows were removed from the trial during lactation due to illness. With these data, and data from their pair-fed EW sows not included, production data from 33 pair-fed EW and CW sows were included in the final analysis. Both total (10.84 ± 0.48) and live born (9.91 ± 0.45) piglets were similar in EW and CW sows, and after litter standardization, sows in each treatment nursed and weaned the same number of piglets (Table 1). Litter growth rate and litter weight at d 14 of lactation were not different between treatments (Table 1), and ADG of the litter to d 14 was not

**Table 1**. Mean (± SEM) litter characteristics for pair-fed early-weaned (EW) and conventionally weaned (CW) sows

| Characteristic | EW (n = 33) | CW (n = 33) |
|---|---|---|
| Standardized litter size achieved | 9.55 ± 0.16 | 9.55 ± 0.16 |
| Weight of standardized litter, kg | 14.3 ± 0.4 | 15.0 ± 0.4 |
| Litter weight at d 14, kg | 40.1 ± 1.2 | 42.6 ± 1.1 |
| Litter size at weaning | 9.48 ± 0.17 | 9.48 ± 0.16 |
| Litter weight at weaning, kg | 40.2 ± 1.2[a] | 66.2 ± 1.8[b] |
| Litter growth rate to d 14, kg/d | 2.1 ± 0.1 | 2.1 ± 0.1 |
| Litter growth rate, d 14 to 24, kg/d | — | 2.4 ± 0.1 |
| Litter growth rate, d 0 to weaning, kg/d | 2.1 ± 0.1 | 2.3 ± 0.1 |

[a,b]Means differ, $P < 0.001$.

affected by cannulation ($P = 0.70$). Litter growth rate from d 0 to weaning was negatively correlated (R = –0.39; $P = 0.03$) to CW sow backfat changes throughout lactation. There was no relationship between the number of piglets weaned and weaning-to-estrus interval (**WEI**), ovulation rate, or ESR ($P > 0.10$).

### *Feed Intake, Body Weight and Backfat Change, and Metabolic Status in Lactation*

There was no difference between treatments in ADFI to d 14 of lactation, whereas overall lactational ADFI differed ($P < 0.0001$) between treatments due to increased feed intake and the longer lactation of the CW sows (Table 2). Cannulation did not affect feed intake to d 7 ($P = 0.75$) or d 14 ($P = 0.76$) of lactation compared with noncannulated sows. Treatment did not affect BW, backfat, or any measures of tissue catabolism at farrowing or at d 14 of lactation (Table 2). However, at weaning, weight change ($P < 0.12$), backfat change ($P < 0.09$), and calculated body fat change between farrowing and weaning ($P < 0.06$) tended to be greater for CW sows. Although EW sows had greater ($P = 0.0006$) backfat at weaning than CW sows, calculated muscle mass and body fat content of sows at weaning were not different. However, when the calculated change in body fat content at weaning was expressed as the percentage of body fat retained from farrowing until weaning, CW sows had a lower percentage of calculated body fat remaining ($P = 0.05$). Both groups of sows were in a similar negative energy balance at the time of weaning.

### *Feed Intake, Metabolic Status, and Body Weight and Backfat Changes After Weaning*

Total feed intake, ADFI, body condition, and metabolic status between weaning and ovulation were not different between treatment groups (Table 3).

**Table 2**. Feed intake, metabolic status, and body condition of pair-fed (n = 33) early-weaned (EW) and conventionally weaned (CW) sows in lactation (mean ± SEM)

| Characteristic | EW | CW |
|---|---|---|
| Farrowing weight, kg | 188.9 ± 2.7 | 190.7 ± 2.9 |
| Weight at d 14, kg | 181.7 ± 2.9 | 183.5 ± 3.1 |
| Weight at weaning, kg | — | 181.5 ± 3.2 |
| Weight change, d 0 to 14, kg | –7.2 ± 1.1 | –7.3 ± 1.1 |
| Weight change, d 0 to weaning, kg | — | –9.2 ± 1.9 |
| Backfat at farrowing, mm | 17.5 ± 0.6 | 17.8 ± 0.7 |
| Backfat at d 14, mm | — | 16.3 ± 0.6 |
| Backfat at weaning, mm | 15.9 ± 0.5[a] | 14.7 ± 0.5[b] |
| Backfat change, d 0 to 14, mm | — | –1.5 ± 0.4 |
| Backfat change, d 0 to weaning, mm | –1.7 ± 0.4[c] | –3.1 ± 0.4[d] |
| Calculated body muscle content at weaning, kg | 56.4 ± 1.1 | 57.3 ± 1.2 |
| Calculated body muscle content change, d 0 to weaning, kg | 2.2 ± 0.6 | 1.7 ± 0.7 |
| Calculated body fat content at weaning, kg | 18.4 ± 0.5 | 17.6 ± 0.5 |
| Calculated body fat content change, d 0 to weaning, kg | 1.4 ± 0.6 | 3.1 ± 0.4 |
| Calculated d 0 body muscle remaining at weaning, % | 96.7 ± 0.9 | 97.9 ± 1.1 |
| Calculated d 0 bodyfat remaining at weaning, % | 92.6 ± 1.9[a] | 86.6 ± 1.6[b] |
| Average daily feed intake to d 14, kg | — | 3.9 ± 0.1 |
| Average daily feed intake, d 14 to 24, kg | — | 5.3 ± 0.2 |
| Average daily feed intake during lactation, kg | 3.6 ± 0.1[a] | 4.4 ± 0.1[b] |
| Energy balance at d 14, Mcal of ME/d | — | –6.0 ± 0.5 |
| Energy balance at weaning, Mcal of ME/d | –5.5 ± 0.5 | –5.1 ± 0.4 |

[a,b]Means differ, $P < 0.05$.
[c,d]Means differ, $P = 0.09$.

**Table 3**. Postweaning feed intake, metabolic status and body condition of pair-fed early-weaned (EW) and conventionally weaned (CW) sows (mean ± SEM)

| Characteristic | EW (n = 33) | CW (n = 33) |
|---|---|---|
| Total feed intake from weaning to ovulation, kg | 10.6 ± 1.0 | 10.8 ± 0.7 |
| Average daily feed intake from weaning to ovulation, kg | 1.6 ± 0.1 | 1.8 ± 0.1 |
| Body weight at estrus, kg | 169.1 ± 2.9 | 166.7 ± 2.9 |
| Backfat at estrus, mm | 15.1 ± 0.6 | 14.4 ± 0.5 |
| Calculated body muscle content at estrus, kg | 52.1 ± 1.1 | 51.8 ± 1.0 |
| Calculated body fat content at estrus, kg | 16.8 ± 0.6 | 16.2 ± 0.7 |
| Percentage of weaning body muscle remaining at estrus | 90.3 ± 0.9 | 90.3 ± 0.6 |
| Percentage of weaning body fat remaining at estrus | 90.2 ± 1.1 | 90.8 ± 0.9 |
| Energy balance at estrus, Mcal of ME/d | 0.18 ± 0.37 | 0.37 ± 0.35 |

### *Reproductive Characteristics After Weaning*

Three of the 33 EW and 2 of the 33 CW sows were anestrous, of which one EW and two CW sows were cannulated. Overall, five of the 30 EW and three of the 33 CW sows bred were not pregnant at slaughter ($P > 0.10$), for estimated conception rates of 85 and 91%, respectively. One of the EW and two of the CW sows bred received only a single insemination; the remainder of the bred sows received two inseminations. Both of the bred EW sows that were not pregnant on d 25 to 37 of gestation received two inseminations, whereas the single bred CW sow that was not pregnant at d 25 to 37 received only one insemination. Ovulation rate, ESR, embryo number, interval between onset of estrus and ovulation, time to ovulation after onset of estrus as a percentage of the duration of standing heat (log transformed data), and the interval from last insemination to ovulation were not different between treatment groups (Table 4). For ovulation rate, data from one sow slaughtered on d 1 for in vitro study was omitted since the ovulation rate (57 corpora lutea) was two SD greater than the mean and was considered an outlier. There was a trend for WEI ($P < 0.06$) and duration of standing heat ($P < 0.08$) to be shorter in CW sows.

### *In Vitro Embryo Developmental Competence*

Initially, 12 EW and 7 CW sows were slaughtered on d 1 of gestation and within 24 h of ovulation; however, only data from 7 EW and 5 CW sows were included in the final analysis. Four EW sows had embryos that had more than two cells at the time of embryo collection and one sow had not ovulated at the time of slaughter. One CW sow had embryos with more than two cells at the time of collection and one sow had a zero fertilization rate. Estimates of in vitro oocyte recovery rate excludes 1 CW sow since only 1 oocyte was recovered, and estimates of fertilization rate excludes 1 CW sow that had zero fertilization; data from these sows were included in the calculation of ovulation rate. However, two EW sows were dropped from the calculation of ovulation rate because one had not ovulated at time of slaughter and the other had 57 corpora lutea and was considered to be a statistical outlier. Recovery rate (log transformed data: $P > 0.05$) and fertilization rates (arcsin transformed data: $P = 0.08$) of oocytes were not different between treatment groups (Table 4).

Sows with embryos beyond the two-cell stage at collection were not included in the evaluation of development in vitro, resulting in data from only 7 EW and 4 CW sows being included in the final analysis. Duration of lactation did not affect ($P > 0.05$; log transformed data) the ability of oocytes to develop to the four- to eight-cell, or morula, stages in vitro. Embryos from only four sows (three CW and one unpaired EW) developed to the blastocyst stage of development in culture (Table 4).

### *In Vivo Embryo Survival*

For the 17 EW and 24 CW sows that were slaughtered on d 25 to 37, two EW and one CW sow were not pregnant, leaving 15 EW and 23 CW sows in the analysis of embryonic survival. Embryo number, ESR, and embryo size (crown to rump length) were not affected by duration of lactation (Table 4). However, conceptuses from EW sows had a lower ($P < 0.0001$) allantoic fluid volume.

### *Relationships Among Production and Metabolic Characteristics*

In the CW sows only, embryo number (Figure 1) and ESR measured around d 28 of gestation (R = 0.56; $P < 0.005$) were correlated with lactational ADFI, total feed intake in wk 3 of lactation (R = 0.49 and 0.55, respectively; $P < 0.02$), and percentage of body muscle retained from farrowing until weaning (Figure 2). Furthermore, although overall significant correlations between embryo number and ESR and energy balance at standing heat, ADFI during the WEI, and total feed intake from weaning to ovulation were established, these correlations largely resulted from the strong correlations established in CW sows (Figure 3).

There were no relationships ($P > 0.20$) between WEI in either EW or CW sows and duration of standing heat (R = –0.14 and –0.24, respectively), ovulation rate (R = 0.03 and 0.15, respectively), or ESR (R = 0.32 and 0.20, respectively). However, in the EW group, WEI was related to embryo number (R = 0.52; $P < 0.04$).

**Table 4**. Postweaning reproductive characteristics, embryo survival to d 28 of gestation, and embryo developmental competency in vitro in early-weaned (EW) and conventionally weaned (CW) sows (mean ± SEM)

| Characteristic | EW | CW |
|---|---|---|
| Day 1 and 28 data combined | n = 33 | n = 33 |
| Ovulation rate | 17.6 ± 0.7 | 18.7 ± 0.6 |
| Weaning-to-estrus interval, h | 120.3 ± 3.3[c] | 112.3 ± 2.6[d] |
| Duration of standing heat, h | 52.4 ± 2.3[c] | 46.3 ± 2.2[d] |
| Last insemination-to-ovulation interval, h | 9.9 ± 1.6 | 9.2 ± 1.2 |
| Interval from onset of standing heat to ovulation, h | 39.0 ± 1.5 | 37.3 ± 1.7 |
| Ovulation time as a percentage of standing heat duration | 77.4 ± 4.2 | 82.4 ± 3.1 |
| Day 28 data | n = 15 | n = 23 |
| Day of slaughter | 29.9 ± 0.7[a] | 28.3 ± 0.4[b] |
| Ovulation rate | 19.2 ± 1.6 | 18.7 ± 0.6 |
| Number of embryos | 11.2 ± 0.9 | 12.2 ± 1.1 |
| Embryonic survival rate, %[e] | 62.5 ± 4.5 | 63.1 ± 5.0 |
| Embryo length, mm | 27.5 ± 0.5 | 24.5 ± 0.2 |
| Allanto-chorionic fluid volume, mL | 165.6 ± 5.5[a] | 188.1 ± 4.2[b] |
| Day 1 data | n = 13 | n = 7 |
| Ovulation rate of sows used in in vitro study[f] | 16.9 ± 1.3 | 16.4 ± 1.5 |
| Recovery rate of d 1 oocytes, %[g] | 80.2 ± 4.2 | 80.2 ± 5.3 |
| Fertilization rate of d 1 oocytes recovered, %[h] | 96.0 ± 2.2 | 88.2 ± 4.7 |
| Embryos developed to morula stage by 144 h, % | 43 ± 11 (n = 6)[i] | 55 ± 14 (n = 2) |
| Embryos developed to blastocyst stage by 144h, % | 21 ± 8 (n = 3)[i] | 0 |

[a,b]Means differ, $P < 0.05$.
[c,d]Means differ, $P < 0.08$.
[e]Comparisons made on arcsin transformed data.
[f]Excludes sow No. 367 data for ovulation rate as ovulation rate greater than two SD of the mean, although data for recovery and fertilization rate were used.
[g]Excludes sow No. 340 from recovery rate statistics, as embryos lost during transfer due to faulty technique; comparisons based on log transformed data.
[h]Excludes sow No. 386 from the fertilization rate statistics since it had a 0% fertilization rate (slaughtered within 6 h of ovulation); comparisons based on arcsin transformed data.
[i]Numbers in parentheses refer to the number of sows with morulae and blastocysts at the end of 144 h of incubation; comparisons for development to morula based on log-transformed data.

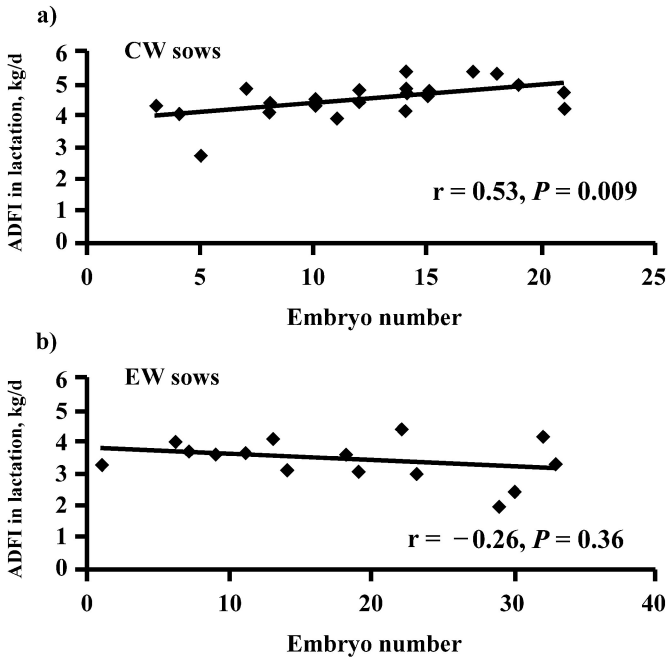


**Figure 1**. Relationship between ADFI (kg/d) in lactation and number of embryos around d 28 of gestation in a) conventionally weaned (CW), and b) early-weaned (EW) sows.

*Plasma Hormone Concentrations*

Initially 17 EW and 17 CW sows were cannulated for endocrine study. However, due to cannula failure, illness, and one EW sow that had an adverse reaction to anesthesia, the final statistical analysis of hormone profiles during lactation included a total of 15 EW and 13 CW sows. Analysis of postweaning hormone profiles included 14 EW and 11 CW sows.

*Intensive Sampling Before and After Weaning*. Time ($P < 0.0001$), but not treatment ($P = 0.36$), affected mean plasma LH over the 20-h period before and after weaning, with no treatment × time interaction ($P = 0.36$; Table 5). Treatment did not affect plasma FSH concentrations ($P = 0.79$), but there were effects of time ($P < 0.0001$) and a treatment × time interaction ($P < 0.0001$) driven by a greater increase in FSH after weaning in EW sows (Figure 4a). Mean plasma IGF-I concentrations in EW and CW sows were 138.2 ± 12.9 and 118.5 ± 7.5 ng/mL, respectively, in the 10-h period before weaning, and 142.2 ± 15.0 and 112.1 ± 6.7 ng/mL, respectively, in the 10-h period after weaning, with no effect of treatment ($P = 0.31$) or time ($P = 0.88$), and no treatment × time interaction ($P = 0.76$).

*Analysis Based on 6-h Samples for the 72-h Period After Weaning*. Data from two CW sows were removed from the analysis of estradiol concentrations after

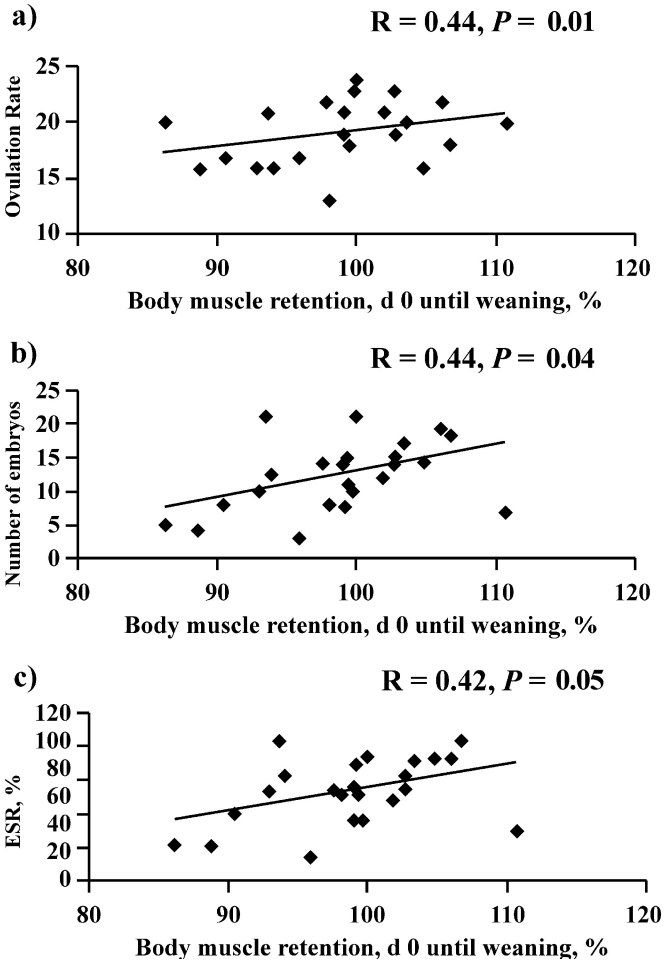


**Figure 2**. Relationship between percentage of body muscle retention from farrowing (d 0) until weaning and a) ovulation rate, b) number of embryos, and c) embryo survival rate (ESR, %) in conventionally weaned (CW) sows.

weaning since the values obtained were considered to be outliers, being greater than two SD above the mean of other sows. Plasma estradiol increased in all sows over the 72-h period of sampling after weaning, but the initial rise in estradiol occurred later in EW vs. CW sows (Figure 4b); consequently, when analysis was based on the first 24-h period of sampling, there were effects of treatment ($P < 0.02$), time ($P < 0.0001$), and a treatment × time interaction ($P < 0.0001$) on plasma estradiol concentrations. Plasma FSH concentrations were initially higher in EW sows, but declined in sows on both treatments over time (Figure 4b); again, when analysis was based on the first 24-h period of sampling after weaning, effects of treatment ($P < 0.03$) and time ($P < 0.0001$) were established, but there was no treatment × time interaction ($P = 0.93$). Plasma IGF-I concentrations were not affected by treatment ($P = 0.46$), time ($P = 0.21$), and there was no treatment × time interaction ($P = 0.78$).

*Analysis of Plasma FSH, LH, and Estradiol Over the Periestrous Period.* The only significant effect on plasma hormone changes through the surge period was a treatment × time interaction ($P = 0.02$) for FSH (Figure 5); the magnitude of the FSH surge, measured as both peak FSH concentration ($P < 0.05$) and estimated total FSH measured over the surge period ($P < 0.08$), was lower in EW sows. Treatment did not affect the magnitude of the proestrous surge of estradiol or of the preovulatory surge of LH (Figure 6). The weaning to peak estradiol concentration and the weaning to peak LH concentration intervals were greater ($P < 0.05$) in EW sows, reflecting a marginally longer WEI in these animals. However, the timing of the estradiol and LH surges relative to the time of insemination and ovulation appear normal and were not affected by treatment (Figure 6). Data from one EW sow were removed from the progesterone analysis since the progesterone concentration 24 h after ovulation was greater than two SD above the mean, and on this basis, was considered to be an outlier. Progesterone concentration 24 h after ovulation was not different between treatments (Table 5).

### *Relationships Among Endocrine and Production Characteristics*

Overall, LH before and after weaning was positively correlated to plasma estradiol after weaning (Table 6). In the CW sows, LH and FSH concentrations were negatively correlated after weaning, as were FSH and estradiol concentrations in EW sows.

Overall, WEI was negatively correlated with plasma LH before weaning. In EW sows, WEI was related to both the change in and concentrations of plasma FSH after weaning, but was negatively correlated to estradiol concentrations after weaning. The interval from peak LH concentration to ovulation was strongly and positively correlated to ESR and embryo number in EW sows. Embryo number was negatively correlated to FSH before weaning in EW sows. Both embryo number and ESR were positively correlated to estradiol after weaning in CW sows and to the interval between the preovulatory LH surge and ovulation in EW sows.

No measurement of IGF-I secretion was related to ovulation rate, ESR, or WEI, but the change in IGF-I after weaning in the EW sows was related to embryo number. Insulin-like growth factor-I did not appear to be related to any measure of body condition in either treatment.

There was no relationship between progesterone concentration 24 h after ovulation and ESR, but progesterone was positively correlated to ovulation rate in the CW sows.

## Discussion

Perhaps surprisingly, the ultimate measures of post-weaning fertility in the present experiment (the number of anestrous sows, conception rate, and the number of embryos in utero around d 28 of gestation in sows

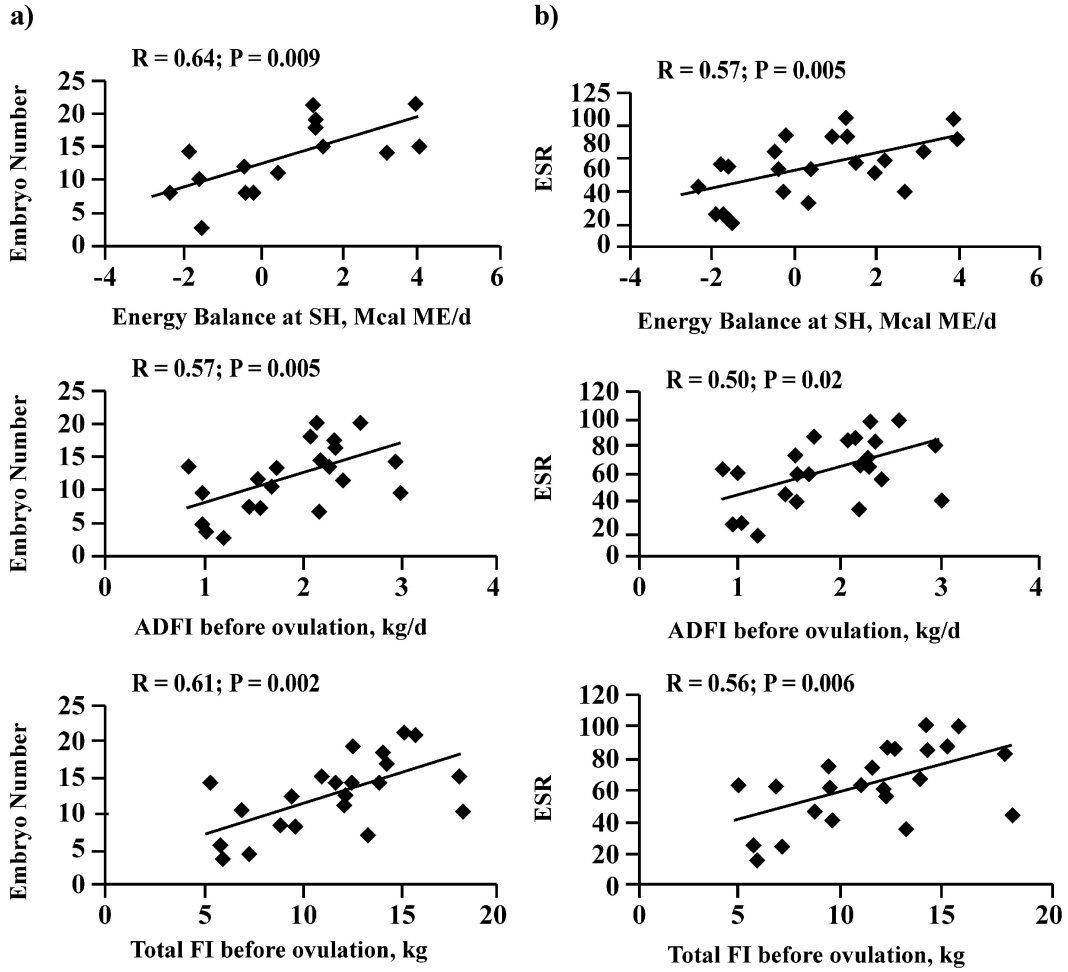


**Figure 3**. Relationship between energy balance (Mcal of ME/d) at standing heat (SH), ADFI before ovulation (kg/d), and total feed intake (FI) before ovulation (kg), respectively, and number of embryos (column a) and embryonic survival rate (ESR, %; column b) in conventionally weaned (CW) sows.

successfully rebred) did not differ between EW and CW sows. The number of sows anestrous after weaning (only 5 of 66) was low, and pregnancy rate of sows bred exceeded 97%, supporting previous suggestions that in contemporary commercial dam-lines, lactational effects on the return to estrus, the ovulatory process, and on fertilization are marginal if good breeding techniques are applied. Nevertheless, embryonic survival in early gestation in both groups of sows appeared to be an important constraint on potential second parity litter size. The results of the present study suggest, however, that the cause of poor embryonic survival differs with the different durations of lactation studied.

Based on the known physiology of the lactating sow, early weaning would be expected to result in reduced fertility due to an inadequate period of postpartum recovery, affecting both the endocrine status of the sow and the integrity of the uterus. Early weaning has been typically associated with a longer WEI (Weitze et al., 1994; Kemp and Soede, 1996; Mabry et al., 1996), consistent with the small but significant 8-h increase in the WEI in EW sows in the present study. A WEI of approximately 5 d is similar to that reported by Xue et al. (1993), Knox and Zas (2001), Corrêa et al. (2002), and more particularly, the data of Mabry et al. (1996) from first parity sows, suggesting that only lactations less than 14 d in duration produce major increases in the WEI. A total of only 11.2 and 12.2 viable embryos in early gestation in EW and CW sows, compared with an average of 10.8 total pigs born in their first litter, suggests that there would be little improvement, or even a decrease, in second litter size if the sows had farrowed their second litter. Overall, if the two lactation strategies are compared, using first litter size and numbers of embryos in utero around d 28 to estimate total pigs born per sow each year, annual productivity of EW and CW sows would be 28.6 and 28.4, respectively. Thus, as suggested in the analyses of Koketsu et al. (1998), the number of litters per sow each year compensates for any reduction in pigs born per litter in sows weaned early, and production criteria other than sow fertility would determine the effectiveness of each lactation strategy.

**Table 5**. Mean (± SEM) plasma LH, FSH, and IGF-I characteristics in early-weaned (EW, n = 15) and conventionally weaned (CW, n = 13) sows during lactation, and plasma LH, FSH, IGF-I, estradiol, and progesterone characteristics after weaning (EW, n = 14; CW, n = 11)

| Characteristic | EW | CW |
|---|---|---|
| Mean LH from –10 to –5 h before weaning, ng/mL | 0.13 ± 0.02 | 0.17 ± 0.03 |
| Mean LH from –5 h to weaning, ng/mL | 0.11 ± 0.01 | 0.18 ± 0.04 |
| Mean LH from weaning to 5 h postweaning, ng/mL | 0.31 ± 0.04 | 0.34 ± 0.05 |
| Mean LH from 5 to 10 h postweaning, ng/mL | 0.34 ± 0.03 | 0.32 ± 0.04 |
| LH pulsatility, 10 h preweaning | 1.27 ± 0.22 | 1.88 ± 0.45 |
| LH pulsatility, 10 h postweaning | 5.50 ± 0.33 | 6.27 ± 0.45 |
| Weaning to LH peak interval, h | 129.7 ± 4.8[a] | 113.8 ± 5.4[b] |
| LH peak to ovulation interval, h | 37.3 ± 1.2 | 37.1 ± 2.4 |
| Total surge LH, ng/mL | 3.55 ± 0.39 | 3.42 ± 0.31 |
| Mean FSH 10 h preweaning, ng/mL | 24.12 ± 3.16 | 28.03 ± 2.96 |
| Mean FSH 10 h postweaning, ng/mL | 43.86 ± 3.54 | 37.12 ± 3.22 |
| Change in mean FSH after weaning, ng/mL | 19.30 ± 3.03[a] | 9.10 ± 1.77[b] |
| FSH peak surge concentration, ng/mL | 20.49 ± 2.56[a] | 43.43 ± 6.52[b] |
| Total surge FSH, ng/mL | 67.83 ± 4.87[c] | 112.81 ± 14.65[d] |
| Weaning to estradiol peak interval, h | 119.9 ± 4.9[a] | 101.3 ± 5.1[b] |
| Estradiol surge peak to LH surge peak interval, h | 10.6 ± 1.8 | 12.6 ± 2.4 |
| Estradiol surge peak to ovulation interval, h | 48.5 ± 1.7 | 49.6 ± 2.8 |
| Total surge estradiol, pg/mL | 223.3 ± 8.7 | 214.6 ± 12.5 |
| Progesterone 24 h post ovulation, ng/mL | 2.62 ± 0.51 | 3.33 ± 0.66 |

[a,b]Means differ, $P < 0.05$.
[c,d]Means differ, $P < 0.08$.

Nevertheless, an improvement in second litter size would have an important impact on overall breeding herd productivity. It is, therefore, of great practical importance to understand the constraints on second litter size in many commercial units. Again, the extensive data accumulated from the present study suggest contrasting causes of reduced fertility in the EW and CW sows, and that management intervention to improve fertility needs to allow for these differences.

Ovulation rate is the first limiting factor for potential litter size, but was not affected by duration of lactation in the present study. Furthermore, compared with ovulation rates of 19.9 in primiparous sows fed normally over a 28-d lactation (Zak et al., 1997a), ovulation rates of 17.6 in EW and 18.7 in CW sows in the present study indicate that duration of lactation did not affect ovulation rate to the extent that it would be a major limiting factor for subsequent litter size.

Irrespective of ovulation rate, a number of studies in primiparous sows have demonstrated detrimental effects of catabolism on follicle quality and oocyte maturation (Zak et al., 1997b; Quesnel et al., 1998b; Yang et al., 2000a), and shorter lactation lengths may produce similar effects. Therefore, based on the experimental approach taken by Novak et al. (2003), we attempted to assess oocyte quality by determining fertilization rates of oocytes recovered immediately after ovulation and their developmental competence in vitro. Sufficient data were available to rule out fertilization failure as a factor limiting the number of viable embryos in utero in either EW or CW sows. Reference to Figure 6 indicates the relative consistency of reproductive events in the periovulatory period. In contrast to the results of Lucia et al. (1999) and Corrêa et al. (2002), there was a marginal effect of lactation length on duration of estrus. In contrast to reports of an inverse relationship between WEI and duration of estrus (Nissen et al., 1997; Lucia et al., 1999), the lack of such a relationship in CW sows in the current study probably relates to a lack of variation in WEI in this population of sows. Critically, the timing of ovulation after the onset of estrus was not different between treatment groups. Ovulation occurred earlier in the estrous period than reported by Knox and Zas (2001), but later than reported by Soede et al. (1994); variations in the frequency of ultrasound measurements and the parity of the sows studied probably explain these differences.

Overall, therefore, lactation length did not influence the key events of the periestrous period that might in other circumstances limit the effectiveness of the insemination protocol adopted. Based on the data from Soede et al. (1995), the interval between the last insemination and ovulation of 9.9 h in EW and 9.2 h in CW sows would be considered ideal. Having inseminated at an ideal time, our data indicate that lactation length did not compromise the ability of the oocytes released to undergo fertilization. Although it is difficult to make any definitive conclusions due to the small number of animals remaining in the analysis, development of fertilized oocytes to the morula stage in vitro did not appear to be compromised by lactation length.

Even though the most of the indicators of sow fertility discussed indicate that modern dam-line sows are increasingly fertile, and under good management conditions, many indicators of fertility are not markedly affected by the duration of lactation, embryonic survival

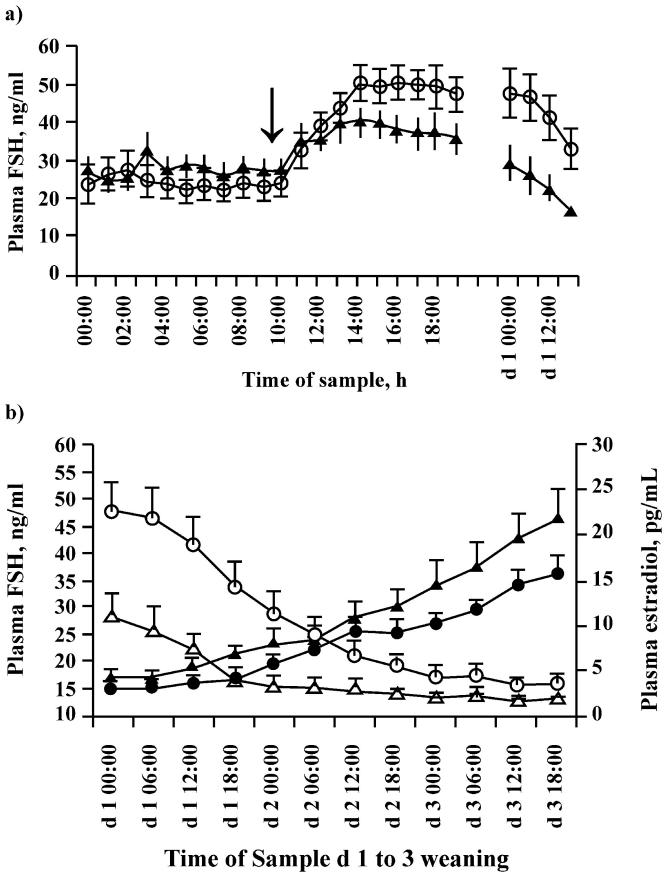


**Figure 4**. a) Mean (± SEM) plasma FSH concentrations measured hourly for 10-h periods before and after weaning (left side of panel) and every 6 h for the 24-h period commencing at midnight on the day of weaning (d 1; right side of panel) for conventionally weaned (CW; triangles; n = 13) and early-weaned (EW; open circles; n = 15) sows. The arrow denotes the time of weaning (1000); b) Mean (± SEM) 6-h period plasma FSH (open symbols and broken lines) and estradiol (closed symbols and solid lines) concentrations measured every 6 h during the 72-h period, commencing at midnight on the day after weaning for conventionally weaned (CW; triangles) and early-weaned (EW; open circles) sows.

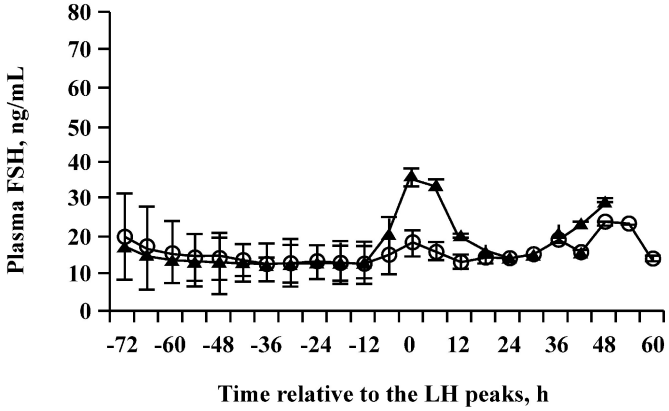


**Figure 5**. Mean (± SEM) 6-hourly plasma FSH concentrations for conventionally weaned (CW) sows (triangles; n = 11) and early-weaned (EW) sows (open circles; n = 14) standardized to the 72-h period before the peak of the preovulatory LH surge (time 0) until the end of sampling.

rates of only 62 and 63% are a constraint on second litter size. Furthermore, in comparable first parity sows in other studies (Zak et al., 1997a), and in recent studies with gilts of the same genotype used in this experiment (S. Town, personal communication), embryonic survival rates of over 80% have been observed, indicating that poor embryonic survival is not an inherent limitation to improved second litter size. The biological basis for the lower embryonic survival seen in the present study is, therefore, of considerable interest.

The low ESR in the EW sows was not unexpected since early weaning has generally been associated with a reduction in ESR. Marsteller et al. (1997) reported that the ESR was reduced in sows weaned at an average of 9.7 d compared with weaning between 18 and 21 d, and ESR in the 18- to 21-d group was similar to that seen in the present study. Whitely et al. (1998) reported an ESR of only 52% in primiparous, crossbred, sows weaned at approximately 21 d of lactation, with an ovulation rate comparable to that seen in present study. In contrast, although Belstra et al. (2002) reported no significant difference in ESR in sows lactating for 13.5 (60% ESR) and 31.5 d (74% ESR), the same trend for poor ESR in early-weaned sows is apparent from their study.

As in the present study, Belstra et al. (2002) reported that lactation length (13.5 and 31.5 d) did not affect embryonic crown to rump length at d 30 postinsemination. Moreover, the reduced allanto-chorionic volume observed in EW sows is consistent with the effects on both amnion volume and embryo weight in sows with a short duration of lactation reported by Belstra et al. (2002).

The endocrine status of EW sows is consistent with the concept that full recovery of the hypothalamic-pituitary-ovarian axis is not complete, and ovarian follicular development is limited when sows are weaned early. Although the number of ovulations, fertilization of the oocytes, and early embryonic development were not different in the present study, the integrity of the oviductal and uterine environment in vivo may be adversely affected by both an incomplete involution process and the lack of adequate stimulation of uterine secretion. Differences in LH secretion before and after weaning were not established, and the robust increase in LH secretion seen in this and other recent studies with commercial dam-line sows (Zak et al., 1997a) contrasts with earlier studies in which greater variability in the LH secretion in lactation and in the LH response to weaning was reported (Shaw and Foxcroft, 1985; Foxcroft et al., 1987). The observed overall inverse relationship between 10-h preweaning mean LH and the WEI in the present study is consistent with earlier reports

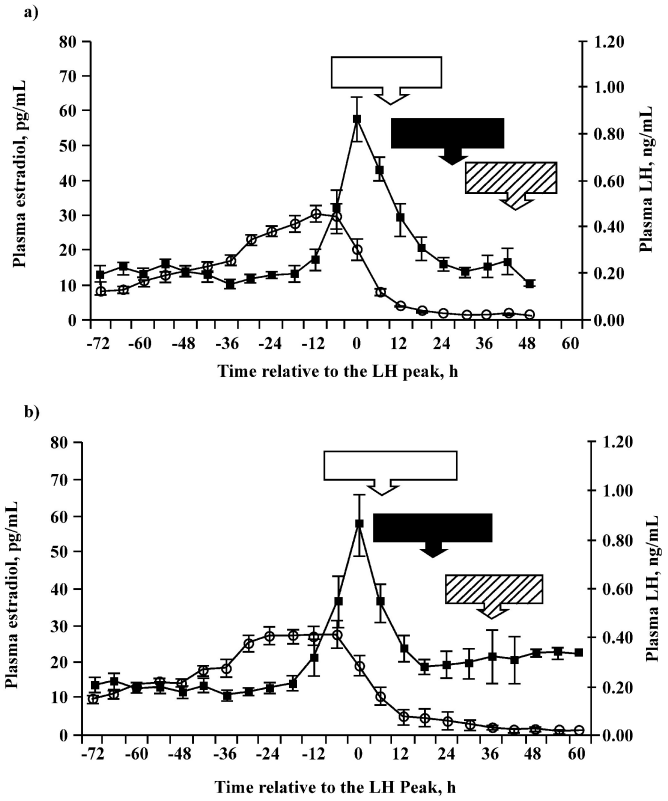


**Figure 6**. Mean (± SEM) 6-hourly plasma LH (solid squares) and estradiol (open circles) concentrations for the 72-h period before the peak of the LH surge (time 0) until the end of sampling for a) conventionally weaned (CW) sows (n = 11) and b) early weaned (EW) sows (n = 14). Relationships between endocrine changes and the onset of standing heat, ovulation, and insemination are indicated. White arrows represent the mean time of the onset of standing heat and timing of the first insemination, with the range represented by the white bar; black arrows represent the mean timing of the second insemination, with the range represented by the black bar, and the hatched arrow represents the mean timing of ovulation, with the hatched bar representing the range.

(Jones and Stahly, 1999; Mao et al., 1999; van den Brand et al., 2000) and suggests that LH secretion is probably a key driver of follicular development in lactation, which in turn determines interval from weaning to the emergence of estrogenic follicles.

In the current study, d 1 postweaning plasma estradiol concentrations were lower, but d 1 plasma FSH was higher in EW sows (Figure 4), and d 1 postweaning estradiol was negatively correlated to d 1 postweaning mean FSH. Taken together, these data suggest a lack of follicular development in the EW sows, with higher FSH on d 1 postweaning resulting from reduced estrogen and inhibin negative feedback from the ovary. This suggestion is consistent with preliminary results from a more recent study in primiparous sows in our laboratory (J. Barry, personal communication), showing that the percentage of sows with follicles >3 mm in diameter increases significantly between d 14 and 16 of lactation. The strong positive correlation between WEI and d 1 FSH and the negative correlation with d 1 estradiol seen in EW but not in CW sows, again supports the conclusion that a lack of follicular development at d 14 of lactation may limit fertility in EW sows. However, despite the longer WEI, the proestrous surge of estradiol in EW sows was equal to that in CW sows, and ovulation rates were similar, suggesting that the status of follicles at the time of ovulation was similar. Since there was also no evidence for differences in fertilization rate or early embryonic development in vitro, an inadequate uterine environment in EW sows may offer the best explanation for a low ESR in this group. The strong positive correlation between IGF-I status after weaning and the number of embryos in utero suggests that IGF-I may be one of the uterotropic factors that is lacking in EW sows with poor embryonic survival.

The difference in the magnitude of the preovulatory FSH surge between EW and CW sows in the present study is considered to be another key marker of incomplete recovery of the endocrine axis. Edwards and Foxcroft (1983a,b) first described a decrease in the magnitude of the preovulatory FSH surge in early-weaned sows and a decreased FSH surge response to an estro-

**Table 6.** Overall substantial correlations between lactation and postweaning endocrine characteristics and reproductive parameters, and within early-weaned (EW) and conventionally weaned (CW) sows

| Characteristic | r-Value | *P*-Value |
|---|---|---|
| Mean LH, 10-h preweaning vs. d 1 postweaning estradiol | 0.37 | 0.07 |
| Mean LH, 10-h postweaning vs. d 1 postweaning estradiol | 0.42 | 0.03 |
| Mean LH, 10-h preweaning vs. weaning to estrus interval | –0.41 | 0.04 |
| LH, 10-h postweaning vs. 10-h postweaning FSH (CW) | –0.59 | 0.03 |
| Mean FSH, 10-h preweaning vs. number of embryos (EW) | –0.77 | 0.03 |
| Change in FSH after weaning vs. weaning-to-estrus interval (EW) | 0.54 | 0.04 |
| Day 1 postweaning mean FSH vs. weaning-to-estrus interval (EW) | 0.53 | 0.04 |
| Day 1 postweaning estradiol vs. d 1 post-weaning mean FSH (EW) | –0.55 | 0.04 |
| Day 1 postweaning estradiol vs. weaning-to-estrus interval (EW) | –0.71 | 0.005 |
| Mean IGF-I, 10-h postweaning vs. embryo number (EW) | 0.79 | 0.03 |
| Progesterone 24 h postovulation vs. ovulation rate (CW) | 0.52 | 0.01 |

gen positive feedback challenge. However, the significant reduction in the magnitude of the preovulatory LH surge in early-weaned sows reported by both Edwards and Foxcroft (1983a,b) and Kirkwood et al. (1984) was not apparent in the present study. This again presumably reflects changes in the endocrine status of contemporary genotypes in response to selection for reproductive merit.

Overall, the endocrine data from the EW sows are characteristic of animals with limited follicular development at weaning and incomplete recovery of the hypothalamic-pituitary-ovarian axis. In the absence of detrimental effects of early weaning on ovulation rate and fertilization rate, it appears that the integrity of the uterine environment may be adversely affected and limits embryonic survival. Since very few of the measures of body condition or metabolic state in EW were associated with embryo numbers or ESR, the metabolic demands of lactation seemed to exert a relatively minor effect on the fertility of the EW sow.

Data from the CW sows suggest that although the recovery of the reproductive axis was more advanced than in EW sows, the metabolic state of CW sows in the critical period before and after weaning may have limited fertility. As expected with the pair-fed regimen imposed, there were no differences in daily feed intake, body condition, or metabolic state during the first 14 d of lactation. Overall, the ADFI of CW sows was greater due to the extra 10 d of lactation; however, as also reported by Belstra et al. (2002), lactation feed intake did not affect ovulation rate. However, strong correlations between feed intake in lactation and ESR and embryo number seen in CW sows but not in EW sows, suggests that nutrient intake and metabolic state were more critical mediators of fertility in the later weaned sows. Effects of increasing catabolism from d 14 to 24 of lactation on subsequent fertility, resulting in the greater change in weight and back fat between farrowing and weaning in CW sows, corresponds well to the period of feed restriction that critically affected embryo survival in studies in both primiparous sows (Zak et al., 1997a) and cyclic gilts (Almeida et al., 2000). Consistent with the data of Belstra et al. (2002), but in contrast to the results of Whitely et al. (1998), embryo survival and embryo number were not related to weight or back fat at weaning.

Although weight loss and back fat loss may give some indication of metabolic state and may be associated with measurable changes in major reproductive traits, recent studies indicate that more subtle measures of body protein mobilization and energy balance may be more closely associated with subsequent fertility. Energy balance of sows at weaning was not different between groups, but in the CW sows, energy balance was related to ESR. Boyd et al. (2000) recommended that back fat loss be limited to approximately 2 mm and that the change in loin eye area be limited to 10 to 11% during a lactation of 18 to 20 d to avoid detrimental effects on fertility. More recently, Clowes et al. (2003) suggested that if muscle protein loss in lactation exceeds 11 to 12% of body protein mass at parturition, reproductive function is impaired. Although CW sows lost over 3 mm of back fat in lactation (approximately 13% of calculated body fat mass at farrowing), and these losses were significantly greater than in EW sows, there was no relationship between these measures and embryo number or ESR. Loss of calculated body muscle mass between farrowing and weaning averaged only 2.5% for the CW sows as a group, which appeared to be well within the limits suggested for effects on fertility. However, as shown in Figure 2, in a subset of CW sows that had the lowest ESR, muscle protein loss was greater than 12%. Therefore, these results support the concept that mobilization of protein mass may be a critical driver of fertility after weaning in primiparous sows, and this may have been a critical factor in the relatively poor embryonic survival in CW sows. Although no measure of IGF-I was significantly different between EW and CW sows in the present study, hormone secretion in the CW sows followed the pattern seen in catabolic sows in previous studies (Zak et al., 1997a; Quesnel et al., 1998a), and at all time points plasma IGF-I was lower in CW than in EW sows.

The metabolic state of the sow between weaning and rebreeding may also be critical for subsequent reproductive performance. Clowes et al. (1994) suggested that the renewed demands of lean growth and the energy requirements of mammary gland involution might be very critical in maintaining an adverse metabolic state after weaning in primiparous sows. In this situation, the energy intake of sows in the weaning-to-rebreeding interval may be critical for improved reproductive performance. Contrary to the results of Carroll et al. (1996), who did not see any improvement in subsequent litter size due to increased feed intake between weaning and estrus, feed intake prior to ovulation affected both ESR and embryo number in CW sows and embryo number in EW sows. These associations are consistent with the positive relationship between energy balance at standing heat and both embryo number and ESR in CW sows, and with the earlier observation of Armstrong et al. (1986) that the size of the second litter was actually related to the sow's energy metabolism 2 to 4 d before the first postweaning estrus.

Overall, the measures of tissue change, feed intake, and litter growth, and the estimates of tissue mobilization and energy balance identified variability in estimated metabolic state and energy balance as key factors limiting the fertility of CW primiparous sows. This further emphasizes the need to adopt management techniques that limit tissue loss in primiparous sows. Weaning earlier in lactation may be another approach for limiting tissue catabolism in primiparous sows; however, the data from the EW sows indicate that fertility-enhancing techniques, such as split-weaning and hormonal treatment, may be needed to achieve acceptable fertility in this situation. Finally, these results confirm that management of feed intake in the weaning-to-re-

breeding period may be critical for the primiparous sow, and yet the design and management of many large commercial breeding facilities may not allow maximal feed intake at this time.

## Implications

Limitations in second litter size in primiparous, early-weaned, sows could not be attributed to low ovulation rate, abnormal endocrine events in the periestrous period, or variable fertilization rates. Rather, indirect consequences of limited follicular development and incomplete recovery of the reproductive axis at weaning seem to be the most likely causes of decreased embryonic survival. In conventionally weaned sows, although poor embryonic survival again seemed to be the primary limitation to second litter size, variability in metabolic state before and after weaning was considered to be the key limitation to improved sow fertility. These results suggest that lactation lengths greater than 14 d can increase potential second litter size. However, with longer lactations, good nutritional management before and after weaning or the use of fertility-enhancing techniques is needed to offset adverse effects of tissue catabolism in a proportion of weaned sows.

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