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Role of Luteinizing Hormone in Primiparous Sow Responses to Split Weaning

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Contents

In 45 primiparous sows, we examined endocrine, ovarian and reproductive responses to split-weaning or five injections per day of 800 ng GnRH from 18 to 21 days of lactation. There was no effect of treatment on absolute or changes in sow weight or backfat depth during lactation. Average piglet growth rates were similar among treatments except that piglets suckling split-weaned sows grew faster ($p < 0.05$) during days 18–21. On day 18, mean plasma LH concentrations and LH pulse frequency remained relatively stable in conventionally weaned sows but increased ($p < 0.01$) in response to split-weaning and GnRH. Prior to weaning on day 21, mean plasma LH concentrations remained elevated in GnRH-treated sows but had returned to control levels in split weaned sows. There was no treatment effect on preweaning LH pulse frequency noted on day 21. Weaning was associated with an increase in plasma LH concentrations in all the treatment groups. Mean plasma IGF-I remained relatively constant in conventionally weaned and GnRH sows, decreased in response to split weaning on day 18 ($p < 0.02$), but were elevated ($p < 0.03$) in split wean sows on day 21. On the day after weaning, split wean sows had more ($p < 0.04$) ovarian follicles ≥3 mm than conventionally weaned sows, with GnRH sows being intermediate. The wean-to-oestrus interval was reduced in split-wean sows compared with those conventionally weaned ($p < 0.01$), with GnRH sows being intermediate. There was no effect of treatment on ovulation rates, numbers of embryos, or embryonic survival rates. These data indicate that split-weaning of litters results in a more rapid return to oestrus after weaning and that this effect is associated with a transient acute increase in circulating gonadotrophins and earlier resumption of ovarian follicular development.

Introduction

The weaning to oestrus interval (WEI) is a major component of total sow non-productive days and, therefore, sow management aims to achieve a relatively short and synchronous WEI. Of potentially greater importance is the observed association between WEI of 6–12 days and subsequent reductions in both farrowing rates and litter sizes (Wilson and Dewey 1993; Vesseur et al. 1994; Steverink et al. 1999). The aetiology of the lower fertility of sows having a relatively long WEI is not known, although it has been demonstrated that a longer WEI is associated with a shorter duration of oestrus and so a shorter interval from oestrus onset to ovulation (for review, see Soede and Kemp 1997). This may make appropriate timing of insemination relative to ovulation more difficult, resulting in reduced fertility.

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A shorter WEI can be achieved with injection of gonadotrophins at weaning although reductions in sow fertility have been observed following insemination at a hormone-induced oestrus (Kirkwood et al. 1998). Non-pharmacological approaches to management of the WEI include split-weaning, which is the weaning of the heavier pigs in a litter a few days before weaning of the full litter. Results reported for effects of split-weaning have been variable, with authors noting either improved performance (Cox et al. 1983; Stevenson and Davis 1984; Vesseur et al. 1997; Tarocco et al. 2000) or no effect (Gilbertson et al. 1989; Rojkittikhun et al. 1990). The reason for variable effects has not been determined but responses are likely influenced by background herd performance. Given the potential adverse effect on fertility of WEI >5 days noted above, the conclusion of Gilbertson et al. (1989) that split-weaning will not enhance sow fertility in the absence of excessive lactation sow weight loss and/or prolonged WEI seems likely.

Excessive lactation weight loss and an associated impairment of sow fertility is more likely in primiparous sows and has been associated with reductions in circulating concentrations of gonadotrophins (Baidoo et al. 1992; Clowes et al. 1994; Zak et al. 1997). Therefore, it is possible that increasing circulating LH concentrations prior to weaning may enhance fertility. Earlier studies have indicated that split-weaning will initiate an acute transient increase in circulating LH concentrations (Grant 1989). It is possible that increases in gonadotrophin secretion may accelerate the recovery of ovarian function, ultimately resulting in shorter WEI and improved fertility. The present study was designed to test the hypotheses that (a) split-weaning will improve primiparous sow fertility and that (b) the improvement is primarily a function of enhanced LH secretion by controlling the metabolic state of split-weaned sows by adjusting their feed intake to allow for the expected reduction in milk synthesis.

Materials and Methods

Animals and treatments

This study was carried out at the Swine Research Unit, University of Alberta, in compliance with Canadian Council of Animal Care Guidelines and with approval from the institutional Animal Care Committee. At farrowing, 45 primiparous PIC Camborough sows were assigned on the basis of bodyweight and live-born litter size to one of three treatments during a 21-day (21 ± 1.5) lactation. Litters were standardized to 9 or 10 (9.6 ± 0.16) piglets within 72 h after birth. Treat-

ments were: (a) split-weaning (n = 16), where litters were reduced to the four piglets with the lowest body weights from 18 days until weaning at 21 days; (b) GnRH treatment (n = 14) where, from 18 to 21 days of lactation, litters remained intact but sows received 800 ng GnRH (Sigma Chemical, St Louis, MO, USA) in 4 ml of saline five times daily either i.v. (n = 11) or i.m (n = 3). The GnRH dose was based on previous experience (De Rensis et al. 1991; Mao et al. 1999) and the injection frequency based on the expected increase in LH pulse frequency in response to split-weaning (Grant 1989). All doses of GnRH were administered between 08:00 hours and 22:00 hours; (c) conventionally weaned sows (n = 15) retained intact litters and received no hormone treatment.

Manipulation of metabolic state

During lactation, sows were allowed to access a diet formulated to provide 13.9 MJ DE/kg, 15.9% crude protein and 0.86% lysine for 60 min three times daily at 08:00 hours, 11:30 hours and 15:30 hours. To prevent split-wean sows coming into an improved energy balance after split-weaning, their feed intakes from 18 to 21 days were restricted based on their metabolic body weight at 18 day and the energy requirements for the growth of the four remaining piglets (based on piglet growth from 14 to 18 days). Water was freely available to the sows and litters throughout the study. Creep feed was not provided. Sow energy balance during the period 18–21 days was determined according to the formula of Noblet et al. (1990).

$$EB_{lact} = (FI \times ED - [22 \times BW + 6.83 \times LG - 125 \times n + 1430])/1000$$

EB_{lact} = energy balance (Mcal ME/d); FI = feed intake (kg); ED = energy density of feed (kcal ME/kg); BW = mean sow body weight over the study period (kg); LG = litter weight gain over the study period (g/day); n = litter size suckled

Sow body weight, backfat depth at the P2 position (65 mm off the midline at the last rib; Scanoprobe II, Scano, Ithaca, NY) and litter weights were recorded at 3, 7, 14, 18 and 21 days of lactation. From final weaning, sows were fed a diet formulated to provide 13.9 MJ DE/kg, 13.7% crude protein and 0.56% lysine at 2.5 times their estimated energy maintenance requirements, based on their body weight at weaning. The morning after first detection of oestrus sow feed intake was reduced to 2.4 kg/day.

Reproductive status and breeding protocols

The day after weaning, numbers of ovarian follicles >3 mm on the left ovary were determined by transrectal ultrasonography (Type 200, Pie Medical bv., Maastricht, the Netherlands) with a 5 MHz multiple scan angle transducer.

Oestrus detection involved exposure to a mature boar for 20 min twice daily at 07:00 hours and 19:00 hours starting the day after weaning. At 12 and 24 h after the onset of oestrus sows were artificially inseminated with 3×10^9 live sperm pooled from the same three, known-fertile boars, specifically designated for use in this experiment. Sows were slaughtered 28 day (28 ± 0.7) after insemination and their reproductive tracts recovered for the determination of numbers of corpora lutea and live embryos.

Blood sampling and hormone assays

At day 11 of lactation, 11 sows per treatment were fitted with an indwelling jugular catheter via their superficial cephalic vein (Mao et al. 1999). Blood (3 ml) was obtained at 15-min intervals from 00:00 hours to 20:00 hours on day 18 and day 21 of lactation, comprising 10-h periods, before and after imposition of treatment at 10:00 hours on day 18 (day 18b and day 18a, respectively) and 10-h periods before and after final weaning at 10:00 hours on day 21 of lactation (day 21b and day 21a respectively). Blood samples were collected into heparinized tubes, centrifuged at $1500 \times g$ for 20 min and plasma stored at −30°C until required for analysis. All samples were assayed for concentrations of LH and hourly samples for concentrations of IGF-I.

Plasma LH concentrations were determined by radioimmunoassay (RIA) in duplicate using the homologous double antibody RIA described by Cosgrove et al. (1991). All treatment groups were represented in each assay and all samples from a sow were analysed in the same assay. Average assay sensitivity estimated as 96.8% of total binding was 0.007 ng/tube. The intra- and inter-assay coefficients of variation (CV) were 6.2% and 9.1% respectively. Plasma IGF-I concentrations were determined in duplicate using the homologous double antibody RIA previously described by Cosgrove et al. (1992). The radio-inert recovery and the intra- and inter-assay CV were 101%, 6.8% and 8% respectively. Average assay sensitivity estimated as 94.8% of total binding was 0.22 ng/tube. The extraction efficiencies were routinely high and plasma concentrations were not corrected for recovery.

Statistical analysis

All data analyses were performed using SAS (1990) (SAS Institute Inc., Cary, NC, USA). For the intensive 20-h blood sampling windows at day 18 and day 21 of lactation, plasma LH concentration was characterized initially with the sliding windows technique of Shaw and Foxcroft (1985). The LH pulse frequency was determined over each 10-h sampling window at day 18 and day 21 before and after imposing treatments. LH pulse was visually appraised according to the criteria established by McLeod and Craigon (1985) and the pulse definition used was that of Cosgrove et al. (1991). Mean plasma LH and IGF-I concentration and average LH pulse frequency were analysed over each 10-h period before and after imposing treatments at day 18 and after final weaning on day 21 of lactation.

All data were collected over five farrowing groups (replicates) and dependent variables (WEI, numbers of corpora lutea, numbers of live embryos and embryo

survival) were analysed for normality using the Wilk–Shapiro test ($p < 0.05$). The embryonic survival data were normalized using a log transformation.

Repeated measures GLM procedure was used to analyse the dependent variables, plasma LH and IGF-I concentration, LH pulse frequency, litter weight, feed intake, body weight, backfat and metabolic state. For these dependent variables, sources of variation were treatment, replicate, sow within replicate × treatment interaction and the repeated measure of day. Analysis of sow body weight, backfat and litter weight at day 18 and day 21 of lactation included body weight, backfat and litter weight at d3, respectively, as covariates. Significant differences among the treatments were determined using sow within replicate × treatment interaction as the error term. In the event of a significant day × treatment interaction, differences amongst days were determined within treatments and differences amongst treatments were determined within days.

Sow body weight change, backfat thickness change, litter growth rate and metabolic status change, WEI, number of corpora lutea, number of live embryos and embryonic survival were analysed using analysis of variance, fitting treatment and replicate as main effects. Sow was the experimental unit and used as the error term. Differences among treatment means were determined using the PDIFF term (p-value of differences).

Results

There tended ($p < 0.06$) to be an overall treatment effect and there was a significant treatment × day interaction ($p < 0.02$) for mean plasma LH concentrations. As illustrated in Fig. 1a, compared with their respective control periods (day 18b), mean LH concentrations increased in response to both GnRH and split-weaning treatments (day 18b vs day 18a $p < 0.01$). Mean LH concentration for GnRH-treated sows remained elevated before final weaning (day 21b), whereas the mean LH concentration for split-wean sows was not different from their control period. In response to weaning, mean LH concentrations increased in all treatment groups when compared with their respective day 18b concentrations ($p < 0.01$) and were elevated ($p < 0.01$) in conventionally weaned and split-weaned groups compared with day 21b.

There tended ($p < 0.07$) to be a treatment effect and there was a significant ($p < 0.01$) treatment × day interaction for LH pulse frequency. The LH pulse frequency at 18 day increased ($p < 0.01$) in response to both GnRH and split-weaning, whereas values for conventionally weaned sows remained unchanged (Fig. 1b). For both the GnRH and split-wean groups, LH pulse frequency at 21 day before final weaning (day 21b) was not different to the control period at day 18b. The very high pulse frequency after weaning precluded accurate analysis for this period.

Plasma IGF-I concentrations remained unaffected by day or treatment in conventionally weaned and GnRH sows (Fig. 1). In contrast, compared with their control period (day 18a), IGF-I concentrations in split-weaned sows were initially reduced ($p < 0.02$) but were then

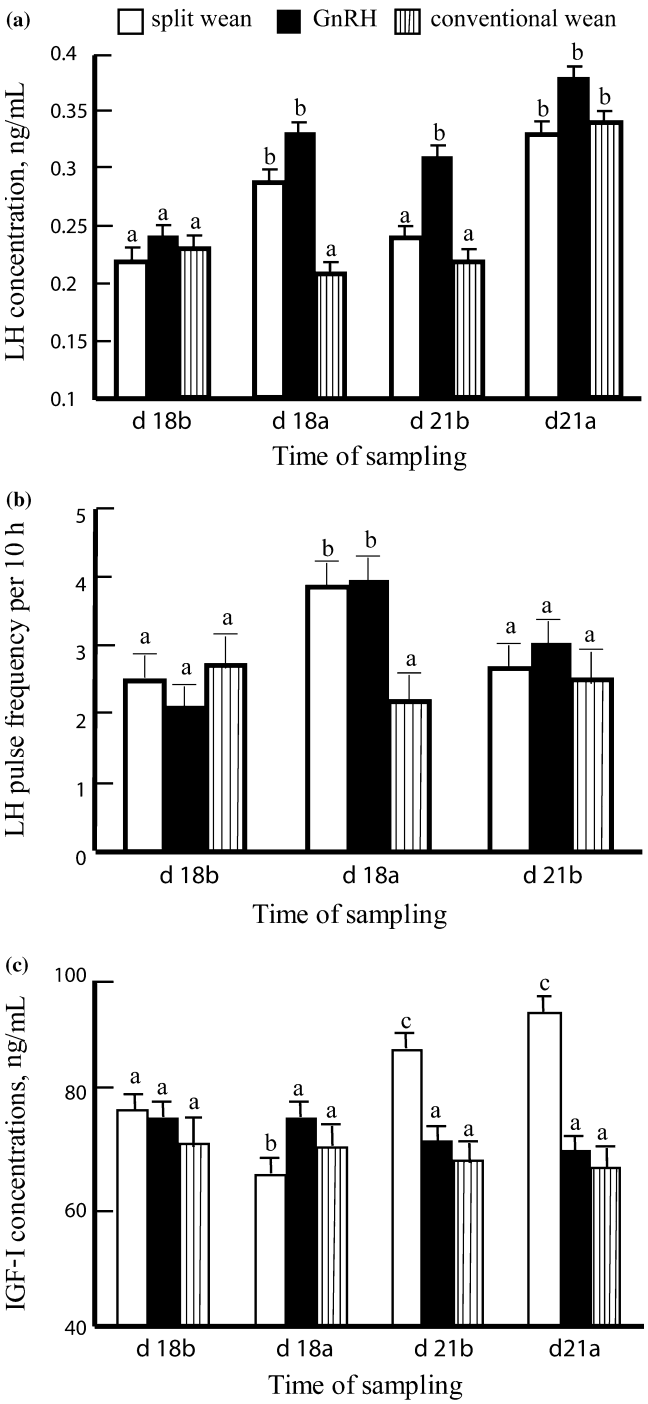

Fig. 1. Effect of split-weaning of litters (n = 11), GnRH treatment of sows (n = 11) or no treatments (conventionally weaned, n = 11) between days 18 and 21 of lactation on plasma concentrations of LH and IGF-I during 10 h before (day 18b) and after (day 18a) imposition of treatments and 10 h before (day 21b) and after (day 21a) final weaning. Data represent mean (±SE) plasma LH concentrations (1a), mean (±SE) plasma LH pulse frequency (1b), and mean (±SE) plasma IGF-I concentrations (1c). (a, b) Treatment means differ ($p < 0.01$) from the pre-treatment period (d 18b)

elevated both before ($p < 0.03$) and after ($p < 0.01$) final weaning (Fig. 1c).

There were no differences among treatments for sow body weight or backfat depth during lactation (Table 1). There was a transient decrease in daily sow feed intake

Table 1. Effect of split-weaning of litters or GnRH treatment of sows on weight and backfat loss, and subsequent sow performance[a]

	Split-wean[b]	GnRH[c]	Conventionally weaned
Number of sows	16	14	15
Sow weight, 3 day lactation (kg)	190.0 ± 1.3	191.1 ± 1.4	192.9 ± 1.3
Sow lactation weigh loss (kg)	9.9 ± 2.0	11.3 ± 2.4	13.4 ± 2.0
Sow P2 backfat, 3 day lactation (mm)	15.3 ± 0.6	15.6 ± 0.8	15.8 ± 0.7
Sow lactation backfat loss (mm)	1.9 ± 0.4	1.9 ± 0.5	2.4 ± 0.4
Energy balance 18–21 days (MJ DE/day)	−29.9 ± 4.7	−32.5 ± 5.1	−29.2 ± 4.9
No. of follicles >3 mm[d]	7.3 ± 0.8a	5.1 ± 1.0ab	4.0 ± 0.8b
Wean-estrus interval (h)	111.0 ± 5.8a	124.0 ± 6.3ab	135.6 ± 5.9b
No. corpora lutea, 28 day gestation	17.7 ± 1.0	16.9 ± 1.1	15.5 ± 1.0
No. live embryos, 28 day gestation	12.8 ± 1.2	10.9 ± 1.4	9.1 ± 1.4
Embryonic survival[e] (%)	64.4 ± 8.4	60.2 ± 9.4	56.1 ± 9.4

[a]Least square means ± SE.
[b]Litter size reduced to four pigs between days 18 and 21 of lactation.
[c]Five injections daily of 800 ng GnRH between 18 and 21 days of lactation.
[d]Measured by transrectal real-time ultrasound examinations of left ovary 1 day after weaning.
[e]Per cent ovulations represented by live embryos at 28 day of gestation.
Means followed by different letters differ; ab $p \leq 0.05$.

immediately following the split weaning (data not shown), although there were no evident differences among treatments for calculated energy balances for the period days 18–21 (Table 1). Litter weights increased in a curvilinear manner ($p < 0.05$) during lactation and were not affected by treatment (data not shown). However, the growth rate between 18 and 21 day of the four piglets remaining on the split-wean sows was greater ($p < 0.05$) than that in intact litters (281 ± 32, 183 ± 36, and 193 ± 33 g/day for split-weaned, GnRH and conventionally weaned litters respectively). Based on litter growth rate, the estimated milk yield of split-weaned sows was approximately 50% of their pre-treatment estimate ($p < 0.05$). Between 18 and 21 days, the within-day estimated milk yield of the split-wean sows was approximately 67% of that of either conventionally weaned or GnRH treated sows ($p < 0.05$).

The number of follicles ≥3 mm recorded the day after weaning was greater ($p < 0.04$) in split-wean sows compared with conventionally weaned sows, with numbers observed in GnRH sows being intermediate (Table 1). The WEI was shorter ($p < 0.01$) for split-wean sows when compared with either conventionally weaned or GnRH treated sows (Table 1). No effects of treatment were detected for ovulation rate ($p = 0.32$), numbers of embryos ($p = 0.16$), or embryonic survival ($p = 0.8$) (Table 1).

Discussion

The data presented indicate that split weaning of litters for 3 days prior to full weaning resulted in a more rapid return to oestrus after final weaning but no effect on ovulation rate or numbers of live embryos. The lack of significant effects of split-weaning on numbers of embryos and embryonic survival rate may be reflecting the relatively few sows assigned to the study, although effects of genotype, parity and season cannot be discounted. Interestingly, although no overall treatment effect was detected, if individual means for numbers of embryos were examined, there appeared to be a trend ($p < 0.07$) for more embryos in the split-weaned group. The improved performance was accompanied by transient increases in both mean LH concentrations and frequency of LH pulses. Previous studies in which a positive effect of split weaning was observed failed to separate potential endocrine effects following acute reductions in litter size from improvements in sow metabolic status due to the reduced metabolic demands of smaller litters (Vesseur et al. 1997; Tarocco et al. 2000). Based on the calculated sow energy balances in the present study, we did appear to be successful in maintaining an equivalent metabolic status across treatments. The initially depressed plasma concentrations of IGF-I were probably a reflection of the transient decrease in feed intake associated with the period immediately following split weaning. However, the higher circulating IGF-I concentrations on day 21 suggest that split-wean sows were less catabolic at weaning. Accepting that metabolic status at weaning can impact subsequent sow performance, it seems that metabolic status cannot be determined solely as a function of energy balance. Even when energy balance is maintained relatively constant, sow metabolic status appears improved by split-weaning. In commercial practice, where feed restriction is not practiced, effects of split-weaning on metabolic status would likely be even more evident. Therefore, we suggest that the observed effects on follicular development, WEI, and possibly also on numbers of embryos, was a function of the acute transient increase in LH secretion, which in turn was a consequence of a reduced suckling intensity. However, the positive effects of increased LH secretion will be facilitated at the ovarian level by improvements in metabolic status. Our data on ovarian follicular development on the day after weaning, and ovulation rate measured at 28 day of gestation, suggest that increased numbers of follicles in the immediate post-weaning period would not be the primary factor increasing potential litter size in split-weaned sows.

It is interesting that the increased LH secretion in split-weaned sows was transient, and LH secretion was similar to that in conventionally weaned sows by the day of final weaning. This observation supports that of Grant (1989), who also noted a transient increase in LH that was nevertheless associated with increased ovarian follicular development at the time of final weaning 7 days later. Therefore, it appears that a pre-weaning elevation of gonadotrophins for a period of <3 day was sufficient to initiate the increased ovarian follicular development observed the day after weaning.

Although we suggest that the driver of improved sow performance in the split-wean sows was the increased LH secretion, it is likely not the sole effector. Both mean LH concentrations and LH pulse frequency were also increased by the GnRH treatment but reproductive responses to this treatment were consistently intermediate between the conventionally weaned and split-wean

treatments. Furthermore, although the 3-day period of GnRH treatment used in the present study did not result in increased LH secretion after final weaning compared with control sows, the marked inhibition of endogenous pulsatile LH secretion after weaning reported by Mao et al. (1999) after 7 days of GnRH treatment was not apparent. Overall, it appears that other responses to split-weaning, in addition to effects on LH, are involved in the expression of improved performance. Although not measured in the present study, recent evidence indicates that a 4-day period of split-weaning also acutely increases circulating concentrations of FSH, while reducing plasma prolactin concentrations (Degenstein et al. 2006). Accompanying an increased LH, these latter changes would be expected to stimulate ovarian follicular development, as was observed in the present study. Interestingly, while the latter study with chronically cannulated sows confirmed endocrine responses to split-weaning and associated improvements in numbers of embryos at 30 day after mating at the first post-weaning oestrus, a companion study in non-cannulated sows failed to establish any improvement in sow fertility in response to the same 4-day period of split-weaning (Wellen 2005; Wellen et al. 2006).

Considering previous literature and data from the present study, we conclude that split-weaning will increase secretion of gonadotrophins and reduce secretion of prolactin, and that these endocrine changes have the potential to accelerate ovarian follicular development and an earlier return to oestrus after weaning. Additionally, split-weaning for periods as short as 3 days can positively impact sow metabolic status, which would enhance the sow responses to changes in endocrine status. Further, we suggest that variable responses to split-weaning noted in the literature reflect a diversity of post-weaning sow performance in conventionally weaned groups. Split-weaning may improve performance of sows exhibiting otherwise relatively poor performance but will not further improve performance of sows having otherwise normal fertility.

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