Ovarian responses to lactation management strategies

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A number of lactation management strategies can be applied to reduce negative effects of lactation on post-weaning fertility. This paper focuses on effects of lactation length, Intermittent Suckling and Split Weaning on follicle development and subsequent oestrus. It is concluded that a lactation length of less than 3 weeks still leads to suboptimal reproductive performance in our modern sows. Further, both Intermittent Suckling and Split Weaning stimulate lactational follicle development and oestrus, but the variation in response between sows still limits practical application.

Introduction

During lactation, both the suckling intensity of the piglets and the negative energy and/or protein balance of the sows normally inhibit the growth of pre-ovulatory follicles and therefore, prevents the occurrence of lactational oestrus. Gonadotrophin release and thus follicle development can be suppressed to such an extent that post-weaning follicle development and subsequent fertility (weaning-to-oestrus interval, ovulation rate, embryo survival and subsequent farrowing rate and litter size) are negatively influenced too. This is most obvious in first litter sows, but is also observed in older parity sows with extensive lactational weight loss (Thaker & Bilkei 2005). A number of lactation management strategies can be applied to reduce negative effects of lactation on post-weaning fertility: optimizing lactation length, Intermittent Suckling (i.e. temporary separation of sows and piglets during the last days of lactation) and Split Weaning (i.e. a reduction of litter size during the last days of lactation). Before reviewing these strategies, a short overview is given of the mechanisms leading to lactational suppression of follicle development.

Lactational suppression of follicle development

This paper briefly describes the most important factors that affect follicle development during lactation, as Quesnel (2009) in this volume focuses on lactational and nutritional influences on follicle development.

Antral follicle development depends on the gonadotrophins LH and FSH. During established lactation, LH-levels and pulsatile LH release are suppressed due to the suckling-induced inhibition of the GnRH-pulse generator (De Rensis *et al.* 1993). The level of LH-suppression is related to the suckling intensity, but also to the negative energy balance of the sows; in

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primiparous sows on a low feeding level, LH-levels were reduced compared to sows on a a high feeding level (e.g. (Quesnel & Prunier 1998; Van Den Brand *et al.* 2000). Effects of lactation on FSH are less consistent, and seem more dependent on ovarian negative feedback (inhibin) than on suckling (reviewed by (Prunier *et al.* 2003).

In the course of lactation, LH-pulsatility normally restores (e.g. Van Den Brand *et al.* 2000), which may be related to a decrease in suckling frequency and intensity or to the increase in pituitary LH response to GnRH (e.g. Bevers *et al.* 1981; Rojanasthien *et al.* 1987). Concomitantly with the increase in LH-pulsatility, follicle size increases in the course of lactation. Thus, with progressing lactation, the follicle pool on the ovaries achieve a greater diameter, but most sows do not develop follicles beyond 3-4 mm until after weaning (Lucy *et al.* 2001), although occasionally sows develop pre-ovulatory follicles (~8mm) and ovulate during lactation.

The inhibition of LH release during lactation influences both lactational follicle development and the resumption of ovarian activity after weaning (Shaw & Foxcroft 1985, Quesnel *et al.* 1998). Additionally, the positive feedback mechanism to oestradiol matures in the course of lactation, increasing the ability of sows to mount a pre-ovulatory LH-surge of sufficient magnitude (Sesti & Britt 1993). These mechanisms together form the basis for lactational effects on subsequent fertility parameters, such as: weaning-to-oestrus interval, ovulation rate and even embryo survival (reviewed by Prunier *et al.* 2003), eventually affecting farrowing rate and litter size.

Lactation management strategies

To counteract negative consequences of lactation on subsequent fertility, several management strategies can be applied. These strategies aim to improve the energy balance of the sows and reduce the intensity of suckling in the last part of lactation either by reducing litter size (Split Weaning) or by limiting the period of suckling (Intermittent Suckling). Since lactation length in itself is a major determinant of post-weaning ovarian activity, it is discussed first.

Lactation Length

In 1982, Varley reviewed effects of day of weaning on subsequent reproductive functioning. He concluded that the weaning-to-oestrus interval was around 7 days when sows were weaned at 3 weeks or beyond, but increased when sows were weaned at less than 3 weeks of lactation. Further, lactation length did not seem to influence ovulation rate or fertilization rate, but embryo mortality around the time of implantation seemed to increase in sows with lactation lengths shorter than 24 days. As a result, subsequent litter size was reduced substantially. The negative consequences of short lactation lengths on litter size were attributed to the compromised uterine development after weaning.

Since the review by Varley (1982), sows have changed substantially. Due to genetic selection, current sows have a higher percentage of lean muscle tissue, a lower level of backfat and improved reproductive performance as shown by the lower percentage of sows with delayed weaning-to-oestrus intervals and increased litter size. So, how does lactation length affect reproductive functioning in modern sows?

Hardly any studies have investigated immediate post-weaning reproductive physiology of sows in relation to lactation length. An interesting exception is the study by (Willis *et al.* 2003) who compared sows weaned at Day 14 with sows weaned at Day 24 of lactation. They found a lower LH-pulsatility pre- and post-weaning, consistent with an HPO that is not fully recovered at Day 14 of lactation. They also found higher FSH levels and a delayed increase in post-weaning oestrogen levels with weaning at Day 14, consistent with a suppressed follicular development at Day 14.

How does suppressed follicle development at weaning affect further reproductive functioning? A few studies have analysed farm data on sow performance in relation to lactation length. These studies show that the weaning-to-service interval is consistently short when lactation length is beyond 21 days, but weaning-to-service interval increases after shorter lactation lengths (see Fig. 1). In sows with short lactations that did not show oestrus by day 6 after weaning, Knox & Rodriguez Zas (2001) consistently found smaller follicles at weaning and at 3 days after weaning, suggesting a suppressed follicle development in these sows.

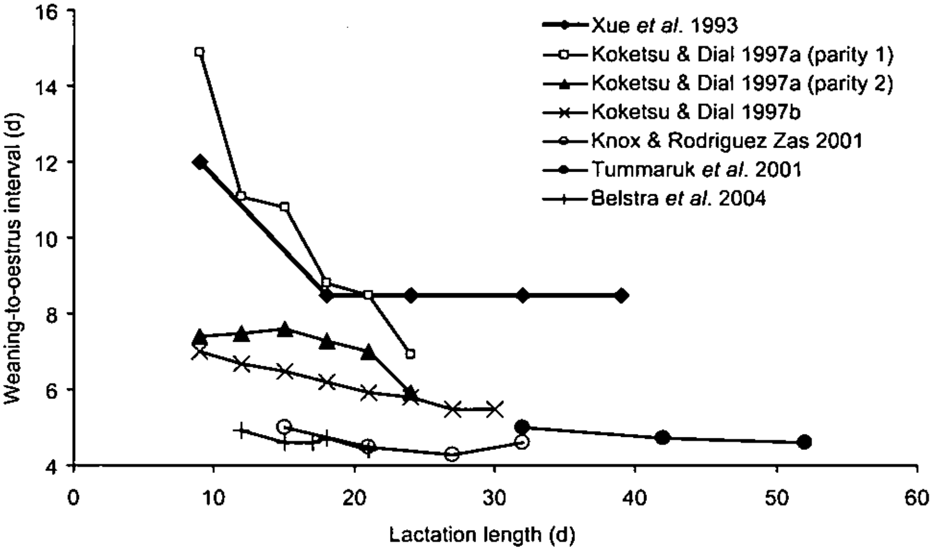

Fig. 1 Effect of lactation length on weaning-to-oestrus interval NB Knox and Rodriguez Zas (2001): only sows showing oestrus within 8 days from weaning. The percentage of sows showing oestrus within 8 days was 35%, 94%, 98% and 96%, for the shortest to longest lactation length classes; Tummaruk *et al.*, (2001): sows with oestrus within 20 days [90.3%; percentages not shown per lactation length class]; Belstra *et al.*, (2004): only sows showing oestrus within 10 days from weaning. The percentage of sows showing oestrus within 10 days was 92%, 92%, 90%, 94% and 98% for the shortest to longest lactation length classes.

Also when oestrus is not delayed, reproductive processes may still be affected. For example, Knox & Rodriguez Zas (2001) found that in sows with short lactation (< 16d), the percentage of sows showing oestrus was reduced (35%), and also the percentage of these sows that ovulated (78%) compared to sows with a longer lactation length (e.g. for sows with a lactation length of 25-31 d: 98% showed oestrus, of which 98% ovulated). The sows that failed to ovulate either showed a short/intermittent oestrus with only small or medium sized follicles or ovarian cysts at that time or had a long oestrus period with normal sized pre-ovulatory follicles that did not ovulate within the first 5 days of oestrus. In ovulating sows, lactation length did not affect follicle size at ovulation. Thus, even when oestrogen production of sows with short lactations is sufficient for oestrous behaviour, the immaturity of the positive feedback system may prevent/disable the occurrence of an LH-surge (Sesti & Britt 1993), and consequently, these sows fail to ovulate. If the LH surge fails in sows with normal sized pre-ovulatory follicles, follicles may become cystic. There are no recent reports outlining the influence of lactation length on the development of cystic follicles or cystic ovaries; Svajgr *et al.* (1974) found that the number of cystic follicles doubled for sows with a lactation length of 13d compared to 24d (1.3 vs 0.6). Consistent with the earlier review by Varley (1982), Willis *et al.* (2003) did not find effects of lactation length on ovulation rate.

A possible disadvantage of longer lactations for farm reproductive parameters can be the increase in the number of sows with lactational ovulation. This may especially occur in multiparous sows from specific prolific breeds, but may occur in any sow with a low number of suckling piglets or a high feed intake during lactation. Lactational ovulation is often not noted and, such sows will thus be marked as 'delayed oestrus'.

Lactation length may also affect subsequent farrowing rate and litter size, as reviewed by Varley (1982). Also in more recent literature, short lactations (less than 3 weeks) negatively affect subsequent litter size and farrowing rate (e.g. Koketsu *et al.* 1997, Le Cozier *et al.* 1997). Further, the limited information that is available on reproductive performance for long lactations seems to indicate a positive influence of lactation lengths above 4 wks, both for farrowing rate (+3%) and litter size (+0.6 piglets) (Gaustad-Aas *et al.* 2004), although such effects are not always found (Tummaruk *et al.* 2001) and may not result in a higher number of piglets per sow per year (Xue *et al.* 1993).

Summarising, especially short lactation lengths (<3wks) have a clear negative effect on post-weaning follicular development and subsequent interval to oestrus, ovulation response and even farrowing rate and litter size. These effects are related to the level at which lactation has suppressed follicle development. Effects of short lactation lengths on weaning-to-oestrus interval seem less evident in recent literature (see Fig. 1), although the true effect is masked by the relatively short cut-off points (e.g. oestrus up to 8 days from weaning (Knox & Rodriguez Zas 2001) and oestrus up to 10 days from weaning (Belstra *et al.* 2004). Nevertheless, such reduced effects of short lactation lengths on weaning-to-oestrus interval may be related with the ongoing selection for short weaning-to-oestrus intervals. However, if this means ovulation of less developed follicles and oocytes, such sows may still have lower subsequent performance.

Intermittent Suckling

One way to reduce the suckling stimulus of the piglets and as such stimulate follicular development and subsequently lactational ovulation, is by introducing daily periods of separation of sows and piglets during the last part of lactation. This procedure is termed reduced or limited suckling, interrupted suckling, or Intermittent Suckling (IS). Recently, Langendijk et *al.* (2006) and Gerritsen *et al.* (2008b) reviewed effects of Intermittent Suckling on subsequent fertility. They showed that the enormous variation in (lactational) oestrous response of sows in the different Intermittent Suckling regimes can be attributed to the regimes used, but also to differences between sows. In short, up to 90% of sows may show lactational oestrus if the Intermittent Suckling does not start too early in lactation (preferably later than Day 18) and lasts for at least 10h per day. During separation, sows should be housed out of sight and hearing from the piglets, preferably allowing some boar contact. The genotype of the sow is of major importance and also the parity, since primiparous sows have a lower oestrous response.

Interestingly, sows that respond to the treatment with oestrus do so in a synchronous fashion at a seemingly normal interval of 4 to 5 days from start of treatment (see Gerritsen *et al.* 2008b). Extending the duration of the treatment period does not seem to influence the oestrous response. As a consequence, a treatment period of 14d compared to 7d (Soede *et al.* 2009) did not significantly increase the oestrous response. Interestingly, in that study, the sows that did not show a lactational oestrus within the period that they were subjected to IS, showed a 'normal' weaning-to-oestrus interval once they were weaned. Thus, the oestrous response of sows in an Intermittent Suckling regime seems to be an 'all or none' phenomenon; either a 'normal' duration of the follicular phase, or no response, as was also concluded by Stevenson & Davis (1984).

Even though a considerable number of sows may show lactational oestrus in an Intermittent Suckling regime, other sows show varying patterns of response in terms of follicle development. In the experiments of Gerritsen *et al.* (2009); Gerritsen *et al.* (2008a) and Langendijk *et al.* (2009), ultrasound was performed daily to check the ovarian response to the Intermittent Suckling regimes. The following follicle development patterns could be distinguished; sows showing follicular growth with follicle diameters not reaching pre-ovulatory size (<6mm) and sows developing follicles of pre-ovulatory size (>6mm). Within the second category, follicles either ovulated, regressed or became cystic (>10mm, not ovulating). Fig. 2 shows the patterns of follicle development for each of these categories. Table 1 shows the number of sows for each of these ovarian response for weaned control sows (Day 21 of lactation) and for sows in which Intermittent Suckling started at Day 14 or at Day 21 of lactation. Failure of sows to develop follicles beyond 6 mm was particularly observed when IS commenced early in lactation (13% for D14 vs 0% for d21), illustrating the recovery of gonadotropic secretory capacity during this period of lactation. Sows with follicular development beyond 6 mm, mostly ovulated and showed oestrus. However, in some sows follicles regressed without ovulation (Table 1). This phenomenon (pre-ovulatory sized follicles regressing) has, to our knowledge not been described before and has not been observed before by our research group. FSH and LH release on the first day of IS did not seem limiting for normal follicle development in these sows (Langendijk *et al.* 2009). Nevertheless, the follicles in these sows were anoestrogenic (no increase in peripheral oestradiol levels) despite an increase in follicle diameter. In sows ovulating normally, an increased concentration of oestradiol was observed from day 2 of IS. We suggest that the follicles that regressed were not fully responsive to the increased FSH and LH secretion after commencement of IS. Some sows that showed pre-ovulatory follicle development (>6mm) developed cystic follicles. Particularly sows that commenced IS at 14 d of lactation were prone to show this deviation in the follicular phase: in 13 % of all D14 sows subjected to IS (vs 0% for D21) all follicles turned cystic, or some follicles became cystic with the other follicles luteinising and forming corpora lutea. The sows with all follicles turning cystic had a normal follicular phase oestrogen rise, but had a very low or no LH surge and (consequently) no signs of luteinisation (no drop in oestradiol, no rise in progesterone), see Gerritsen *et al.* (2008b).

Table 1. Follicle development[1], ovulation and oestrus response [between brackets] in Intermittent Suckling regimes with 12h daily separation starting at day 14 (IS14) or day 21 of lactation (IS21)[2]

	Treatment		
	Control[3]	IS14	IS21
	N=36	N=79	N=23
Follicular development remained <6mm	0% [0%]	13% [0%]	0% [0%]
Follicular development reached >6mm			
Ovulation within 8d after start IS/wean	94% [a] [100%]	66% [b] [90%]	87% [b] [95%]
No ovulation			
Regression of follicles	0 [0%]	9% [0%]	13% [100%]
Cystic follicles	6% [100%)	13% [80%]	0

[1]Daily ultrasound from onset of IS or from weaning onwards
[2] Results are based on (Gerritsen et al. 2009; Gerritsen et al. 2008a; Langendijk et al. 2009);
[3] Control sows weaned at Day 21 of lactation
[ab] $P<0.05$

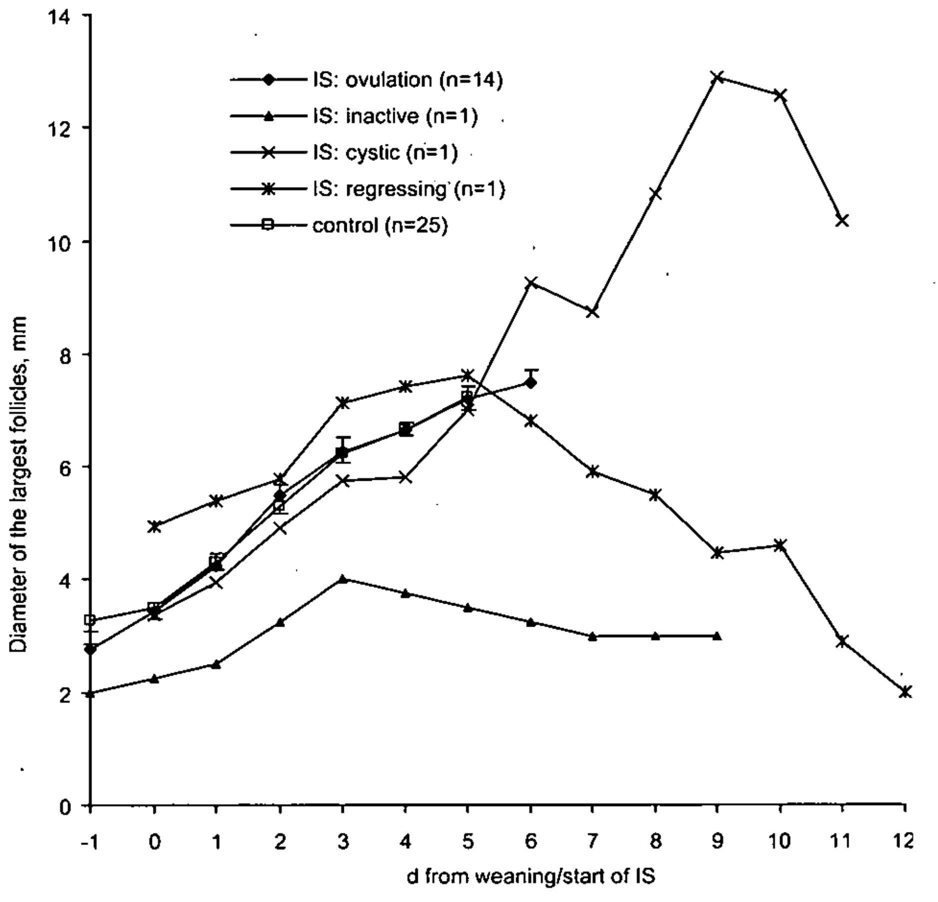

Fig. 2 Different patterns of follicle development in sows during the last day of full lactation (full lact) and after subsequent weaning (Control) or onset of Intermittent Suckling (IS). In IS, the majority of sows the follicles reached ovulatory size (>6mm) and subsequently ovulated (IS:ovulation), but in others follicles never reached ovulatory size (IS:inactive, one example sow shown) or did reach ovulatory size and either developed cystic ovaries (IS:cystic, one example shown) or follicles regressed (IS: regressing, one example shown). [Langendijk, unpublished results].

This again illustrates that during early lactation, the postive feedback of oestradiol on the LH surge centre is still developing or there is insufficient LH to induce an adequate LH surge.

In the early studies on Intermittent Suckling, the majority of sows ovulated after weaning. Thus, from those studies it remains unclear if and how Intermittent Suckling and/or lactational inseminations affect pregnancy. Recent Intermittent Suckling studies (reviewed by Gerritsen *et al.* 2008b), suggest that pregnancy rate, embryo survival rate and embryo development are negatively affected if IS-induced ovulation takes places around Day 19-21 after farrowing (IS started at Day14) and IS continues after ovulation, which may be related with lower progesterone levels in these sows. When sows are inseminated more than 3 weeks after farrowing, neither litter size, nor farrowing rate are negatively affected by lactational inseminations in an IS-regime (Soede *et al.* 2009) or during 'normal' lactation (Gaustad-Aas *et al.* 2004).

Summarizing, recent studies with Intermittent Suckling show that there is a large variation in oestrous response, in which specifically the onset of treatment, the genotype of the sows and parity of the sows is important. The oestrous response is an 'all or none' phenomenon, which means that sows either show oestrus after a follicular phase of normal duration or do not respond at all and show a normal return to oestrus after weaning. The majority of sows that show oestrus, normally ovulate with a normal ovulation rate, even though in some sows follicles may become cystic. When sows ovulate during an intermittent regime, they have a similar chance of becoming pregnant and remaining pregnant and a similar litter size compared to sows that are inseminated post weaning, but the negative effects of short farrow-to-insemination intervals also hold for Intermittent Suckling.

Split weaning

With Split Weaning, the suckling stimulus of the piglets is reduced and the energy balance of the sows is improved by the permanent removal of a part of the litter a few days before complete weaning. In the different studies reported, there was a considerable variation in the Split Weaning regimes; Split Weaning lasted for 3 to 7 days before complete weaning, leaving 2 to 6 piglets for the remaining lactation which lasted 17 to 35 d. Matte *et al.* (1992) reviewed the reproductive performance of split wean sows and concluded that the reduction in the interval from weaning to oestrus was mostly affected by the number of piglets that remained with the sow during the last days of lactation. The largest reduction in weaning-to-oestrus interval was seen when only 3 piglets remained with the sow for 4.7 days. Interestingly, Grant (in: Varley & Foxcroft 1990) showed that effects of Split Weaning (leaving 5 piglets with the sow) on both LH levels and follicle development after 7 days of treatment were larger when the 6 anterior teats had been covered compared to when only Split Weaning was applied. Since piglets had a similar growth rate in both treatments, and thus the metabolic demands on the sows were similar, it appears that effects on LH and follicle development are primarily mediated by the neural stimulation of suckling. Only few experiments have since evaluated effects of Split Weaning on reproductive physiology or performance of sows and these later experiments have all focused on the lower parity sows (Mahan 1993; Vesseur *et al.* 1997; Zak *et al.* 2008; Foxcroft et al. unpublished results). These studies also consistently show that the weaning to oestrus/insemination interval is reduced when Split Weaning is applied. Two recent studies have evaluated the role of the gonadotrophins in this effect. Degenstein *et al.* (2006) showed that during the whole period of Split Weaning (day 16-19), prolactin levels were reduced and FSH levels were increased. Further, Zak *et al.* (2008) found an acute increase in LH levels and LH pulse frequency in the 10h following Split Weaning at day 18. At the day of weaning (3 d later), average LH levels were similar to the control animals, both before and after final weaning. The day after weaning, split wean sows had more follicles with a diameter larger than 3 mm. Thus, the increased LH levels, the higher FSH levels during the split-wean regime and possibly the lower prolactin levels together stimulate follicle development and shorten weaning-to-oestrus intervals.

As far as we know, hardly any information is available on the quality of ovulation in split weaned sows. However, the reproductive characteristics that have been measured show a slightly increased ovulation rate (17.7 compared to 15.5 (Zak *et al.* 2008)), a similar embryo survival rate at day 28 (64% versus 60% (Zak *et al.* 2008)); similar subsequent litter size (Vesseur *et al.* 1997), and increased farrowing rate in parity 2 sows (97% versus 86% (Vesseur *et al.* 1997)).

Thus, removing the majority of the litter for the last 3-5 days of lactation consistently shortens the weaning-to-oestrus intervals through a stimulation of follicular development, primarily by a reduction in suckling stimuli. The improvement in weaning-to-oestrus intervals is only seen in groups of sows with an otherwise extended weaning-to-oestrus interval. Further, the few papers that have investigated Split Weaning effects beyond oestrus are not very conclusive. Therefore effects on subsequent fertility remain unclear.

Table 2. Oestrus response in recent Split Weaning studies

Split wean (d before weaning)	Litter size before split-wean	Remaining piglets	Lactation length (d)	Parity	WOI[1] (d) (compared to Controls)	Source
7	9.8	4	30	1+3	3.1 (C: 6.6)[2]	(Mahan 1993)
7	10.3	6	28	1	5.6 (C: 5.9)[3]	(Vesseur *et al.* 1997)
7	10.5	6	28	2	4.6* (C: 5.4)[4]	(Vesseur *et al.* 1997)
3	9.6	4 (lightest)	21	1	4.6* (C: 5.7)	(Zak *et al.* 2008)
3	NM	5 (lightest)	19	1+2	4.9 (C: 5.2)	Foxcroft *et al.* (unpublished)

* $P<0.05$, NM not mentioned
[1] WOI = Weaning-to-Oestrus interval
[2] Control sows were weaned at Day 23
[3] of sows that showed oestrus within 15d after weaning (52% and 58%)
[4] of sows that showed oestrus within 15d after weaning (62% and 63%)

Concluding remarks

As shown above, lactation management strategies such as Intermittent Suckling and Split Weaning may stimulate lactational follicle development and thereby postweaning oestrus onset by the combined effects of a reduced suckling intensity (most important) and improved energy balance of the sow. However, the benefits seem rather marginal in our modern sows that have been selected for short weaning-to-oestrus intervals and still not all sows will respond to the treatment. Concerning effects of lactation length, also for our modern sows, a 3-week lactation still seems to be required for optimal post-wean performance.

Besides applying optimal lactation management strategies, negative consequences of lactation on post-weaning fertility can also partly be counterbalanced by optimizing post-wean management, e.g. by boar stimulation and nutritional management. However, since the post-weaning follicular period is normally very short, even optimal post-wean conditions may not be sufficient to optimize post-lactional fertility. Another possibility would be to allow sows to recover from lactation by postponing post-wean oestrus and insemination e.g. by short term use of a progesterone analogue.

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