Gradual adaptation to weaning of piglets: intermittent suckling and extended lactation

Marieke Berkeveld

Introduction

Under (semi-)natural conditions, piglets are gradually weaned during a long lactation period with complete weaning occurring around 12 to 17 weeks of age [8] [20]. Supervised by the sow, piglets become acquainted with nutrient sources other than sow milk and, with nursing frequency decreasing, they start consuming an increasing amount of solid feed. During this period, the young piglets make a gradual transition from a diet based on sow's milk to a nonmilk diet, ultimately achieving nutritional independence from the sow. This transition coincides with profound changes in intestinal function, enabling the digestion and absorption of nutrients from novel food sources. Hence, under these (semi-) natural conditions, weaning is considered to be a long, gradual process rather than an event that takes place at a specific moment in time.

Over the last decades, the duration of the suckling period under farm conditions has been shortened dramatically. In conventional European pig husbandry piglets are weaned at a young age of 3 to 4 weeks. Conventional weaning is associated with an abrupt dietary change from sow's milk to dry feed, reallocation from the farrowing pen to a nursery pen, maternal deprivation, and often mixing with unfamiliar pen mates. Since the change to (nutritional) independency is a rather abrupt one, and takes place at a young age, piglets are physiologically not fully competent to deal with this situation. As a result, conventional weaning is often associated with a decreased nutrient intake, a reduced piglet growth [39], display of piglet distress behaviour [12], and changes in gut integrity and function after weaning that increase the susceptibility for diarrhoea [48]. Considering the detrimental effects of conventional weaning on postweaning performance of piglets, it is desirable to improve their adaptation to weaning.

Considering the gradual weaning process under natural conditions, an obvious adjustment of husbandry conditions to resemble the natural weaning process would be to extend the suckling period. Under conventional housing conditions, an older age at weaning increased the postweaning feed intake [28], attenuated the postweaning growth reduction [28], reduced the development of stereotypic behaviour [30], and attenuated the weaning-associated villous atrophy [11] and the detrimental effects on intestinal function [33]. Improving piglet postweaning performance by extending lactation length can only be profitable if reproductive performance of sows is not compromised. However, the inhibitory effect of suckling and the metabolic constraints on ovarian activity and ovulation during a prolonged continuous lactation will delay the establishment of the next pregnancy of the sow.

During intermittent suckling (IS), sow and piglets are temporarily separated for a number of hours each day during the second part of lactation. This management strategy mimics the increasing amount of time spent away from the piglets during the lactation period, when sows themselves can control contact with their piglets [8] [51]. Limiting the nursing time, when applied by IS, during the lactation period was found to induce ovulation during lactation [29]. Moreover, IS has been shown to improve piglet preweaning creep feed intake and to result in an improved postweaning piglet performance [21] [24] [35], although some studies failed to show a beneficial effect of IS on postweaning performance [18] [31]. The impact of IS seemed to vary between different studies, which presumably was related to the variation in age at onset, separation interval and duration of IS (piglet age at weaning) in those studies.

Hence, an extended lactation combined with intermittent suckling seems to be a promising strategy to encourage piglets to ingest solid feed during the suckling period, and to result in more mature piglets that are more capable of coping with the transition to weaning. Moreover, it is anticipated that sow reproductive performance will not be compromised by the extended lactation, since the onset of IS was shown to induce cyclicity of the sow, resulting in a lactational oestrus during the ongoing suckling period [15].

Figure 1. Removal of sow

In several studies we investigated how an extended lactation combined with IS regimens differing in separation interval, age at onset, and duration affected the adaptation to weaning, by measuring piglet growth and feed intake both during the suckling period and after weaning [3]. An overview of the intermittent suckling regimens applied in the separate studies is given in Table 1. Since enforced maternal separation is associated with behavioural (and physiological) changes [24], one may question whether the repeated maternal separation of piglets subjected to IS also evokes such changes. Hence, we also investigated the effect of IS on piglet behaviour [4].

IS regimen	Age at onset	Duration	Daily separation time	Weaning age
IS6	14 days	~ 4 weeks	2 x 6 hours	43 ± 1 days
IS12	14 days	~ 4 weeks	12 hours	43 ± 1 days
IS14-S	14 days	~1 week	12 hours	21.8 ± 0.4 days
IS14-L	14 days	~ 4 weeks	12 hours	39.9 ± 0.3 days
IS21-S	21 days	~1 week	12 hours	27.8 ± 0.3 days
IS21-L	21 days	~ 4 weeks	12 hours	46.9 ± 0.4 days
IS19-7D	19 days	1 week	10 hours	26 days
IS19-14D	19 days	2 weeks	10 hours	33 days
IS26-7D	26 days	1 week	10 hours	33 days

IS = intermittent suckling; IS6 = IS with 6-h intervals; IS12 = IS with 12-h intervals; IS14-S = IS from d 14 and weaned at d 21.8 ± 0.4 (n = 17); IS14-L = IS from d 14, weaned at 39.9 ± 0.3 (n = 17); IS21-S = IS from d 21, weaned at 27.7 ± 0.2 (n = 14); IS21-L = IS from d 21, weaned at 46.9 ± 0.4 during an extended lactation (n = 16); IS19-7D = IS from d 19, weaning at d 26; IS19-14D = IS from d 19, weaning at d 33; IS26-7D = IS from d 26, weaning at d 33 [2].

Table 1. Applied intermittent suckling (IS) regimens, differing in separation interval, timing and duration

At present, most parameters used to investigate the effects of weaning on piglet gut characteristics are end-point measurements, for which one needs to sacrifice the piglets. We aimed to monitor

postweaning intestinal function in the same piglets, whether or not subjected to a IS regimen, for a prolonged period of time. Hence, we have investigated selected parameters of interest, i.e. 1) intestinal blood flow [2], and 2) plasma citrulline and intestinal fatty acid binding protein (I-FABP) concentrations that might enable us to monitor postweaning intestinal function longitudinally [6]. Results from this study indicated that plasma citrulline was reduced by weaning and was positively correlated to sugar absorption values at day 4 postweaning [6]. Hence, it was postulated that plasma citrulline concentration might be a possible marker of postweaning intestinal function [5]. In one of our studies we investigated the effect of IS regimens differing in timing and duration on postweaning intestinal morphology, besides effects on piglet feed intake and growth [5]. In addition, the effect of IS on postweaning plasma citrulline concentrations was determined and the relation to postweaning intestinal morphology was investigated [5].

Effects of separation interval on piglet feed intake stimulation

Previous studies indicated that the onset of IS at 14 days of age was associated with a reduction in growth during the suckling period, and concomitantly resulted in lower weaning weights of IS litters (weaned around 4 weeks of age) compared to continuously suckled litters [25] [26]. In these studies, piglets and their dam were separated for 12 consecutive hours per day. We supposed that dividing total separation time over 2 intervals might (partly) prevent this reduction in growth, while still stimulating creep feed intake. Indeed, subjecting piglets to two 6-hours separation intervals attenuated, but did not prevent, the reduction of growth after onset of IS compared to a single separation interval of 12 hours [3]. However, we estimated that piglets maintained a greater dependency on milk for their growth in the two times 6 hours regimen compared to a single separation interval of 12 hours, which became evident from the lower feed intake stimulation, the higher nursing frequency, and the activity of the litter that was more synchronized to the presence of the sow [3] [4]. Subjecting piglets to IS with a separation interval of 4 hours from 10 days of age until weaning (d 21) has been shown to result in an improved postweaning feed intake compared to continuously suckled piglets, but no difference was found if the latter were also offered creep feed during the suckling period [18]. Moreover, no difference in weaning weight was observed between intermittently or continuously suckled piglets with or without supplementary feed in the same study. It was demonstrated [37] that separating piglets from their dam for 6 hours per day in the last week before weaning (at 3 to 4 weeks of age), without providing creep feed, did not affect litter weight at weaning. This indicates that piglets subjected to IS are capable to (partly) compensate for the resulting milk intake deficit in the remaining hours with access to the sow. As a result, shorter separation intervals will most probably tone down the piglet's motivation in their search for nutrient sources other than milk. A recent study [31] indicated that separating sow and piglets for 7 hours per day during the last 2 weeks before weaning (day 28) did not improve creep feed intake of piglets during lactation at all, when compared to continuously suckled piglets [31]. Furthermore, our studies indicated that subjecting piglets to 1 week of IS before weaning did increase feed intake when a separation time of 12 hours was used (IS between day 14 and 21), but not with a separation time of 10 hours (IS between day 19 and 26), although piglets were 5 days older in the latter experiment [5].

In conclusion, these data indicate that the duration of a separation interval is of great importance for the stimulatory effect of IS on feed intake, and more so than the total separation time of sow and litter per day. Similar observations were made in a sow controlled housing system, where piglets of sows that spent more time away from their litter had a greater creep feed intake during the suckling period [42].

Figure 2. Piglets in nursery pen without sow

Effect of timing and duration of intermittent suckling on piglet performance

Extending lactation length

As described before, an older age at weaning was found to increase the postweaning feed intake [28], attenuated the postweaning growth reduction [28], reduced stereotype behaviour [31] and weaning-associated villous atrophy [11] and attenuated the detrimental effects on intestinal function [33]. On the other hand, a longer lactation period associated with an older weaning age postpones the next pregnancy of the sow. Combining the extended lactation with IS was hypothesized to improve postweaning piglet performance, while maintaining a similar sow reproductive performance compared to conventional weaning management.

In previous studies on IS as an alternative lactation management strategy, it was mostly applied during a conventional lactation period of 3 to 4 weeks [21] [24]. Subjecting piglets to a short period of IS between 14 and 25 days of age resulted in a reduced piglet growth and concomitantly lower weaning weights compared to continuously suckled piglets [25] [26]. In the same studies, IS piglets were found to have an improved feed intake and growth in the first week after weaning compared to conventionally weaned piglets, which compensated for their lower weaning weights [25] [26]. Similarly, we observed a reduced growth of litters during IS (between d 14 and 21) and lower weights at the time of weaning [5]. In addition, our results indicated that weaning of piglets after a short period of IS resulted in a reduced postweaning piglet growth when compared to still intermittently suckled piglets at that time. Hence, although a short period of IS was found to improve postweaning piglet growth compared to conventionally weaned piglets [25] [26], the IS piglets still experience a reduction of growth after weaning when compared to intermittently suckled piglets [5]. To conclude, a short period of IS commenced at 14 days of age, only partly prevented the growth reduction after weaning.

We hypothesized that when an extended lactation period is combined with IS, the older age at weaning together with a higher creep feed intake before weaning might be even more advantageous to prevent the detrimental effects of weaning on piglet performance. Indeed, extending the lactation length to 6 weeks in combination with IS from day 14 of age, markedly reduced the postweaning growth check compared to that of conventionally weaned piglets [3]. Moreover, growth of these IS litters in the first week postweaning was only slightly lower compared to their growth during the week before weaning [3] [5]. In addition, feed intake in the first week postweaning was only slightly lower compared to IS litters which had already been weaned 3 week earlier (only 1 week of IS) [3] [5]. Altogether, this suggests that piglets subjected to IS from 14 days of age during an extended 6-week lactation period are more capable to cope with the postweaning situation, as judged by their feed intake and growth, than piglets which were weaned after a short period of IS from day 14 of age. It was suggested that the applied IS regimen, once daily for 12 hours (IS12) or separated twice daily for 6 hours (IS6), and thus limited suckling, contributed to the increased preweaning feed intake, considering the higher feed intake observed in IS12 litters [3]. However, the beneficial effects of IS during an extended lactation on postweaning performance observed in our studies cannot be attributed entirely to the limited time for suckling. The older age at weaning could also have contributed to the improved postweaning performance.

Figure 3. Return of sow

Piglet age at onset of intermittent suckling

The initial contact of piglets with nutrient sources other than milk often is attained through exploration of the environment. Exploratory behaviour at d 17 of age, however, was found to constitute only 5% of the total observations in continuously suckled, conventionally housed piglets, whereas 18% consisted of suckling behaviour [4]. The dependency on milk as predominant nutrient source at this young age becomes evident from the low feed intake levels of continuously suckled piglets observed in the first weeks of lactation [3] [5] [40] [45]. Although feed intake behaviour was stimulated when piglets were subjected to IS at 14 days of age compared to continuously suckled piglets [4], feed intake in the first week of IS was still rather low and quite variable between litters [3] [5] [21] [22]. Moreover, piglet growth was reduced after onset of IS at 14 days of age [3] [5], which is in line with previous findings [25] [26]. These results indicate that piglets at this young age are not yet capable to compensate their reduced nutrient intake from milk (due to the imposed limited nursing time) with a sufficient level of dry feed intake. On the one hand, this might be caused by the fact that piglets are not yet acquainted sufficiently with dry feed. However, continuously suckled piglets were found to have 1 to 30 visits to the piglet feeder at day 13 of age [24]. Nevertheless, we and others suggested that this exploration of the piglet feeder was not nutrient driven, given the high number of nursings observed at this early stage of lactation [4] [24] [45]. On the other hand, the gastrointestinal tract, which is still under morphological and functional development at this young age and fully adapted to digestion of sow's milk, might not yet be capable to digest and absorb nutrients from the ingested dry feed.

Postponing the onset of IS with 1 week, to the age of 21 days, increased piglet feed intake about 3-fold in the first week of IS [5]. In contrast, feed intake of litters subjected to IS between day 19 and 26 of age was not greater compared to that of continuously suckled litters in the same period [5]. However, as mentioned previously, the shorter separation time (10 h/d) as applied in this study might have played a part in this lack of feed intake stimulation [5]. Postponing the onset of IS to 21 days of age, irrespective whether or not it stimulated feed intake, was still associated with a reduced piglet growth (around 30% growth reduction), similar to that observed when IS was commenced at day 14 [5]. Postponing the onset of IS with another week (onset at day 26), however, appeared to attenuate the reduction in growth associated with the onset of IS [5]. Piglet growth in the latter treatment was

only reduced with 5% in the first 2 days of IS and with 17% between day 2 and 7 after onset of IS [5]. Moreover, feed intake in the first week of IS was increased 3-fold, compared to litters in which IS began at a 1 week younger age (339 g versus 104 g per piglet, respectively) [5].

In conclusion, we demonstrated that an increased piglet age at onset of IS increases the extent to which feed intake is stimulated. Moreover, if piglets are subjected to IS at a young age, normally associated with low voluntary feed intake, the increased dry feed intake is not adequate to compensate for the deficit in milk intake due to the limited nursing time. However, it needs to be emphasized that even a short period of IS at a young age (11 days, from d 14 onward) can still be sufficient to improve piglet growth and feed intake in the first week after weaning, compared to conventionally weaned piglets [5] [25] [26].

Figure 4. Just a nice piglet

Duration of intermittent suckling in relation to age at onset

Extending the lactation to 6 weeks, with a 4-week period of IS from d 14 onward, resulted in a gradual adaptation to weaning, as judged by the markedly reduced postweaning growth check and a growth and feed intake (shortly after weaning) similar or slightly lower than that in piglets which already had been weaned 3 weeks earlier [3]. However, feed intake in the first week of IS (d 14 to 21) was very low and variable between litters [3]. As mentioned above, postponing the onset of IS to an older age resulted in greater stimulation of feed intake. Indeed, when the onset of a 4-week IS period was postponed to 21 days of age (IS21-L), feed intake during the first week of IS (and in the weeks thereafter) was similar to that of litters already experiencing two weeks of IS at that time (IS14-L; [5]). Moreover, the estimated relative contribution of dry feed to energy intake was similar for both treatments (IS14-L and IS21-L) during the successive weeks of IS, suggesting that dependency on milk was similar for age-matched piglets, despite differences in the experienced duration of IS. This indicates that the extent to which piglets subjected to IS are able to replace the deficit in milk intake (due to the limited nursing time) with ingestion of dry feed, is age-dependent rather than depending on the duration of IS already experienced in the preceding period. It is reasonable to assume that the age-related maturation of the gastrointestinal tract [11], and thereby the ability to process ingested dry feed, might in part be responsible for this effect.

Subjecting piglets to a shorter period of IS, during one week from 14 days of age, instead of the above mentioned 4 week period, still improved preweaning creep feed intake, but weaning of these piglets resulted in a period of reduced growth compared to piglets still intermittently suckled at that time [5]. Combining a short period of IS with an older age at onset of IS (21 days instead of 14 days of age) improved preweaning creep feed intake and shortened the period of reduced growth observed after weaning [5]. The concomitant older age at weaning increased the estimated relative contribution of dry feed to energy intake in the week before weaning from about 14% for piglets weaned at 3 weeks to 27% for piglets weaned at 4 weeks of age. One week of IS between 19 and 26 days of age did not attenuate the growth check observed in conventionally weaned piglets (72 ± 13% and 90 ± 7%, respectively) nor did it improve piglet feed intake in the first 2 days after weaning. Hence, the piglets were probably still too dependent on milk for nutrient intake to prevent a postweaning growth check. However, the piglets subjected to IS did show an improved feed intake and growth later in the first week postweaning. These findings are in line with results of [25] [26] [27], who demonstrated that a short (11-day) period of IS before weaning at 26 days of age improves piglet growth and feed intake in the first week after weaning.

Postponing the onset of IS with another week, and thus extending lactation length with one week (IS from day 26 to 33), markedly reduced the growth check in the first 2 days postweaning (to 32 ± 19%),

when compared with litters weaned one week earlier (72 ± 13%; [5]). This effect was ascribed to the older age at weaning and to the higher stimulation of feed intake associated with the older age at onset of IS. Piglet growth and feed intake in the first two days after weaning was improved even more when piglets had been subjected to a 2-week period of IS before weaning (day 33; [5]). In these litters, growth check in the first two days was markedly reduced (to 11 ± 18%). In addition, it was suggested that the relative growth derived from feed in week 5 of lactation (with 2 weeks of IS from d 21) was estimated to be approximately 47% [5]. Interestingly, these values seem to correspond well with the estimated growth from feed (45%) and with the growth check (14%) reported for litters weaned at 6 weeks of age, after being subjected to a 4-week period of IS [3].

In conclusion, it is suggested that piglets submitted to IS and weaned at a conventional age (3 to 4 weeks) are not yet fully capable to cope with weaning, as judged by piglet growth and feed intake [5]. However, when weaned at an older age (extended lactation) even a short (1-week) period of IS was found to result in a more gradual adaptation to weaning.

Figure 5. Nursing piglets

Intermittent suckling and piglet behaviour

Maternal deprivation can cause behavioural and physiological changes in piglets, such as an increased call rate or inhibition of GH secretion, which often contribute to the survival of the offspring during periods of maternal absence [23]. Moreover, weaning of piglets was found to be associated with the development of behavioural patterns indicative for piglet distress, such as aggression, belly nosing, manipulation of pen mates and (in)activity [12]. Since the submission of piglets to an IS regime imposes them to (repeated) periods of maternal separation, it was questioned whether IS is associated with similar behavioural changes.

Onset of IS resulted in a transient increase in activity of piglets on the first day compared to continuously suckled piglets, with a more pronounced effect in litters separated from their sow for 12 consecutive hours than for two times 6 hours [4]. We suggested that this increase in activity might have been the result of the restlessness commonly associated with a sudden (previously unexperienced) separation from the mother. Besides a higher activity, piglets subjected to IS had vocalized more compared to continuously suckled piglets, but this was observed predominantly on the first day of IS. Later in lactation, an increased call rate did occur, but only when one entered the farrowing room shortly before the sows were returned to their litters (personal observations). The fact that the increased activity was transient and not observed anymore at 2 days after the onset of IS, suggests that the piglets quickly habituated to the periods of maternal absence. Our results corroborated data by [24] who observed no differences in piglet non-feeding-related activity between IS and continuously suckled piglets (both selected on a high feed intake level during lactation) on the third day after commencement of IS. Although total daily activity was not affected by IS (except for the first day), the activity pattern of the litters over the day was changed dramatically [4]. Activity of IS litters coincided closely with the presence of the dam, even more so when litters with two 6-hour separation intervals were compared to those with one 12-hour separation interval. This became evident from the higher percentage of activity during sow's absence in the latter litters. Again, this is in agreement with findings of [24] who found lower activity levels of IS litters during separation from their dam compared to continuously suckled litters in that period of the day.

Nutritional, social and environmental stressors are suggested to play a part in the development of belly nosing behaviour [10] [14], a stereotypic behaviour, involving repeated rhythmic up-and-down massage movements with the snout at the flanks or belly of penmates, often observed after weaning

of piglets. The repeated maternal deprivation during IS from 14 days of age did not result in development of belly nosing behaviour during the 6-week suckling period [4]. In contrast, conventional weaning of piglets at day 21 under identical housing conditions did result in an increased expression of this behaviour after weaning [4]. This suggests that complete weaning is necessary to induce this stereotypic behaviour, since the alternately presence and absence of the sow during IS did not evoke such a behavioural response.

Separation of piglets from their dam at weaning, without mixing them with unfamiliar penmates, induces an increase in aggressive behaviour [13]. It was demonstrated that subjecting piglets to IS during an extended lactation did not affect the proportion of aggressive or manipulative behaviour during the suckling period [4]. Similarly, the time spent on aggressive and manipulative behaviour in litters submitted to IS between day 14 and 25 of age was similar to that of continuously suckled litters in that period [24]. Likewise, at 4 weeks of age no effect of sow controlled housing was observed on the percentage of aggressive behaviour when compared to piglets in conventional housing [46]. Although the sows are not forced to leave their litter in sow controlled housing systems, the total separation time of sow and piglets increased with increasing piglet age from 25% at 2 weeks of age to 75% at the time of these behavioural observations at 4 weeks of age [46]. Interestingly, plasma cortisol concentrations of piglets in sow controlled housing were found to be similar to conventionally housed piglets throughout the suckling period [46]. However, only 1 blood sample was taken (at 9:00 in the morning 2 weeks before weaning) during the entire suckling period, and more frequent sampling is desirable to study possible effects of maternal deprivation on cortisol concentrations in more detail. In conclusion, it is suggested that IS (maternal deprivation) was not associated with lasting behavioural patterns indicative of piglet distress during the suckling period [4].

An increased number of vocalizations in response to weaning was observed both in conventionally weaned as well as IS litters, although this response seemed to be somewhat delayed for the latter (personal observations). Hence, we questioned whether piglets submitted to IS are already accustomed to the separation from their dam at the time they are weaned. If so, repeated maternal separation during the lactation period might attenuate the weaning-associated behavioural (and physiological) changes observed in conventionally weaned piglets by us and others [4] [5]. The present study does not provide any data on behaviour of IS piglets after weaning and other studies on this topic are scarce. In an attempt to unveil possible effects, two studies investigating the effect of previously experienced maternal separation on postweaning behaviour are discussed [5].

Time spent on exploratory, manipulative or aggressive behaviour in the first 2 days postweaning was found to be similar in IS and conventionally weaned piglets [24]. Moreover, no differences in non-feeding related activity were observed between IS and conventional litters at their first day postweaning. However, as suggested by the author, these data should be interpreted with care since results were obtained using only a small number of litters. Similar to IS before weaning [24], the periods of maternal absence in sow controlled housing did not affect the percentage of active, exploratory or aggressive behaviour of piglets at day 3 postweaning compared to conventionally housed piglets [46]. Moreover, no differences were observed in postweaning plasma cortisol concentrations [46]. Results of these studies suggest that the postweaning behaviour of piglets that experienced repeated periods of maternal separation during the lactation period is not different from that of piglets kept conventionally during lactation. We do want to emphasize that piglet behaviour was only observed shortly after weaning in the latter studies and some behavioural patterns associated with piglet distress, like belly-nosing, are rarely seen in the first days after weaning, but develop several days thereafter [13]. Since no data is currently available on the possible long-term effect of previously experienced periods of maternal separation (either by IS or sow-controlled housing) on postweaning behavioural or physiological traits, this remains to be elucidated.

Effect of intermittent suckling regimens on gut characteristics

Preweaning period

Fasting has dramatic effects on small intestinal mucosal structure and function. Overnight nutritional depletion was found to result in an increased intestinal permeability and decreased villous height in humans [50]. The onset of IS (at 14 to 19 days of age) was associated with only a small, insignificant nutrient intake during the periods of sow absence, given the low feed intake levels of piglets during the first 2 days of IS [3] [5]. Hence, this indicates that piglets are imposed to repeated periods of (almost) fasting shortly after the onset of IS. One might hypothesize that these periods of underfeeding negatively affect small intestinal structure and/or function, as occurs with weaning. Yet, subjecting piglets to a single, short-term fasting of 6 or 12 hours was not associated with any detrimental effects

on intestinal morphology [19]. But, IS piglets are subjected to repeated nonsuckling (and low nutrient intake) periods. [35] demonstrated that IS for 8 h/day without supplementary feeding between 3 and 5 weeks of age (hence repeated 8-h fasting periods), did not induce changes of intestinal function or net fluid absorption of the small intestine at weaning, when compared to continuously suckled piglets. Although piglets submitted to IS initially have a low feed intake and are limited in their nursing time, their body weight gain in the first two days after onset is only 26% lower than that of continuously suckled piglets [5]. Moreover, a normal mucosal proliferation and intestinal growth was found in 1-week old piglets when their enteral nutrient intake was reduced by 40% accomplished by parental feeding [10]. The results from the above studies seem to indicate that IS, although associated with a reduced nutrient intake at the onset, does not negatively affect intestinal structure or function per se.

Provision of creep feed during a continuous lactation was not associated with changes in small intestinal structure or absorption values at 21 days of age [16] [17]. It must be stated however, that in the latter study total feed intake of piglets during the lactation period was, as can be expected at this young age [45], rather low with an average of 236 g per piglet (ranging from 0 to 363 g per piglet). In a study of [9] creep feed was supplemented with chromiumoxide (consumption of which colours the faeces green), which enabled the authors to designate individual piglets as good eaters, moderate eaters or non-eaters. In line with the above mentioned findings, the consumption of creep feed (eaters) did not affect morphology of the small intestine at 28 days of age when compared to non-eaters. Again, creep feed intake during the suckling period varied greatly between litters, with an average of 301 g per piglet (ranging between litters (containing both eaters and non-eaters) from 24 to 690 g per piglet). Although the supplementation of chromium-oxide allows one to distinguish between eating and non-eating piglets within litters, individual ingested creep feed could not be quantified in the study of [9]. We suggest that preweaning feed intake might still have varied considerably between individual piglets designated as good or moderate eaters in the latter study, and this might have made it difficult to establish an evident effect of preweaning feed intake on intestinal morphology. Hence, more research is needed studying the effect of the creep feed quantity ingested by individual piglets and its effect on their intestinal development.

In accordance with the above mentioned studies using 3 or 4 week old suckling piglets [9] [16], villous height in the small intestine of piglets weaned around 32 days of age, was not affected by the supplementation of creep feed [34]. Moreover, subjecting piglets to IS from 2 weeks before weaning, to stimulate food intake during the suckling period, did not affect villous height at weaning [35]. These findings seem to corroborate the absence of a significant difference in villous heights of piglets subjected to IS before weaning (day 26) compared to continuously suckled piglets in our study [5]. It must be noted, however, that villous height in the small intestine of these IS piglets was reduced (though not significantly) at weaning compared to continuously suckled piglets. It was hypothesized that this might have been caused by the withdrawal of milk (and its trophic factors) during the periods of sow's absence and by the fact that the applied IS regimen in our study [5] did not result in a greater feed intake during the suckling period compared to continuously suckled piglets. Similarly, subjecting piglets to a 2 week period of IS without supplementary feed intake also resulted in a non-significant reduction of villous height at weaning [35].

Providing supplementary creep feed to continuously suckled piglets did not affect crypt depth of the small intestine at 3 to 4 weeks of age [9] [16]. However, deeper crypts were found in supplemented continuously suckled piglets around 32 days of age [34]. Moreover, subjecting piglets to IS with supplementary creep feed during the suckling period resulted in deeper crypts at the end of the suckling period compared to continuously suckled 32-day old piglets [35]. Similarly, we observed a non-significant increase in crypt depth in intermittently suckled piglets at the end of the suckling period [5]. So, based on the studies above, one might conclude that supplementation of creep feed itself already affected intestinal morphology (crypth depth) during a 5-week lactation period (but not during a 3-week lactation period). But, subjecting piglets to 2 weeks of IS before weaning at 5 weeks seemed to reinforce this effect, resulting in a greater crypt depth compared to similar-aged continuously suckled piglets.

Postweaning period

One or two weeks of IS combined with an extended lactation (weaning at day 33) prevented the villous atrophy observed in piglets on the second day after conventional weaning and resulted in deeper crypts at day 2 and 8 postweaning as compared to piglets weaned at day 26 [5]. One might question whether this effect is solely due to the increased piglet age at weaning or whether the IS regimen also contributed to this effect. Conventional weaning was imposed only at day 26 of age, since an extended lactation length (without IS) would have compromised sow reproductive performance [5]. As

a result, the beneficial above described effects on postweaning intestinal morphology observed in the IS litters of this study could not be specifically ascribed to either the older age at weaning (33 days) or to the subjection to IS. Other investigators [11] reported that postponing weaning from 3 to 5 weeks of age attenuated, but did not prevent a weaning-associated villous atrophy (65% and 27% reduction in villous height at day 3 postweaning, respectively). Likewise, a 10% reduction was reported in villous height at day 4 after weaning of piglets at 32 days of age and this reduction in villous height was associated with lower net absorption values during a small intestinal segment perfusion (SISP) test [35]. A two week period of IS with supplementary feeding before weaning at day 32 prevented both the postweaning villus atrophy, with longer villi at day 4 postweaning compared to preweaning values, and the reduction in net absorption observed in continuously suckled piglets [35]. Furthermore, postweaning feed intake was positively correlated to villous height [5] [47] and net absorption [27], indicating the importance of feed intake for a proper intestinal function. Interestingly, subjecting piglets to two weeks of IS without supplementary feeding did not induce the above described beneficial effects on postweaning intestinal morphology and absorption [35]. Together, these results seem to indicate that the absence of postweaning villous atrophy observed in piglets weaned after an extended lactation combined with 1 or 2 weeks of IS [5] was predominantly caused by an improved feed intake, stimulated by the limited nursing time before weaning.

Like with 1 or 2 weeks of IS before weaning at day 33, one week of IS before weaning at day 26 of age was found to prevent the weaning-associated villous atrophy observed in conventionally weaned piglets at 2 days after weaning [5]. This was quite a remarkable and unexpected result, given the fact that the preweaning feed intake and feed intake in the first 2 days postweaning were not increased, and that the growth check in the first two days after weaning was not reduced in these IS piglets [5]. At first sight, these findings do not seem to be compatible with the above mentioned observations [35], which suggested that the beneficial effects of IS on postweaning intestinal structure were mediated by a higher preweaning (and consequently postweaning) feed intake. However, similarly to our findings, continuously suckled piglets in the study [35] showed a significantly decreased villous height at day 4 postweaning compared to preweaning values, whereas the IS piglets without supplementary feed did not. This suggests that beneficial effects of IS might not solely be mediated by the increased feed intake. A possible explanation could be that IS piglets are habituated to separation from their mother at the time they are weaned definitively. An attempt to eliminate nutritional stress at weaning by feeding piglets a high level of sow's milk attenuated but did not completely prevent the weaning-associated villous atrophy [47]. Moreover, overnight maternal separation was found to be associated with elevated basal cortisol levels in piglets [22]. In addition, weaning of 19-days-old piglets appeared to activate stress signalling pathways, which mediate and contribute to the intestinal dysfunction, i.e. increased small intestinal permeability, associated with weaning [32]. Therefore, piglets habituated to repeated maternal separation in the IS regimen may have benefited by experiencing less of a stress response after weaning, preventing or attenuating intestinal damage.

Intermittent suckling in perspective

Getting closer to natural weaning

As described before, nursing frequency of litters under conventional housing conditions remains high up to weaning. This is most probably due to the confinement of sows in farrowing crates, preventing them to get away from the demanding litter. The high nursing frequency during the lactation period coincides with a low voluntary creep feed intake at the time piglets are weaned (3 to 4 weeks of age). The abrupt dietary change at weaning, together with altered housing, mixing and sudden separation from the dam, often result in a reduced nutrient intake, reduced growth, impaired intestinal function and altered piglet behaviour. Hence, it is desirable to alleviate the constraints of piglets in their adaptation to weaning.

In the past decade, organic pig farming has gained more interest. One of the regulations of organic pig farming according to the EU legislation is an extended lactation period of at least 40 days. Despite the extended lactation, weaning of piglets kept under organic farming conditions coincided with a stasis in growth and the occurrence of postweaning diarrhoea [7]. So, there is still plenty of improvement to be made. It was indicated that an extended 6-week lactation period combined with IS markedly reduced the postweaning growth check observed in conventionally weaned piglets, Hence, the application of IS on organic farms might be an effective way to improve postweaning piglet performance, ultimately leading to a gradual transition to weaning. Additionally, it might improve the reproductive performance of sows at organic farms, given the occurrence of lactational oestrus after commencement of IS [15].

In current organic farming and in the IS studies, sow and piglets are confined in their farrowing pen

during the entire lactation period. Alternative housing systems, however, providing piglets the opportunity to mingle with other piglets before weaning in a communal piglet area, reduced aggressive behavior after mixing [52]. Moreover, it reduced the number of nursings and increased postweaning feed intake [52]. Combining a communal piglet area with sow controlled housing was found to increase preweaning creep feed intake and improved postweaning feed intake and growth of piglets [51]. Piglets kept under the latter housing conditions during lactation, fought less when mixed at weaning [51]. In addition to the beneficial effects on postweaning piglet performance, sows also benefited from the system. The nursing frequency decreased considerably during the 4-week lactation and sows consumed less food during lactation, but had similar bodyweight losses and weaning-to-oestrus intervals compared to conventionally housed sows [51]. Moreover, it was stated that the welfare benefits to the sow were even more substantial [44]. Sows can leave their litter at will and reduce the udder stimulation, e.g. when their litter is large or when their condition is poor, and participate in the more complex social environment of the get away area [44].

Figure 6. Group of housing sows

The disadvantage of a sow controlled housing or loose housing system, however, is the large variation by which the contact with the litter is reduced by the sow during the lactation period [41] [44]. Hence, a housing system that could regulate the time sows spent away from the piglets, would most probably reduce the variation between litters in terms of nursing frequency, preweaning creep feed intake and growth of piglets. A possible way to regulate this might be to impose the period of time spent away from the litter on the sows by subjecting them to IS. Results of our research group [5] [15] [24] demonstrated that applying IS during the (extended) lactation period was associated with above mentioned benefits for piglets (increased preweaning feed intake and improved postweaning performance) and their dam (reduced number of nursings). Hence, the application of IS in “sow controlled” housing (i.e. group housing of sows during the separation interval, combined with a communal piglet area) could possibly improve the benefits of this lactational management even more. It would most probably also reduce the variation observed in sow controlled housing. In our studies IS was applied using a standard separation interval (10 or 12 h) during the suckling period [5]. Given the increasing time spent away from the litter during the lactation period when contact is controlled by the sow, one might ask to what extent a more gradual increase of the separation interval (h/day) might further improve the above proposed application of IS.

Intermittent suckling and gut health

Piglets of herds with a history of postweaning diarrhoea generally have shorter villi and deeper crypts compared to piglets of a SPF herd, and these effects are even more marked in herds where diarrhoea is associated with mortality [34]. Both rotaviruses and *Escherichia coli* were demonstrated to be important in the aetiology of diarrhoea in these piglets at weaning [36]. Hence, in a subsequent study [35] studied the effect of the exposure of the small intestine to ETEC on small intestinal net absorption during a SISP test. The latter study demonstrated that exposure to ETEC reduces the net absorption of the small intestine at weaning and thereafter compared to the unexposed small intestine. Moreover, subjecting piglets to IS with supplementary feeding during the suckling period attenuated the reduction in small intestinal absorption after ETEC exposure. These results might indicate that IS could also have a beneficial effect on postweaning intestinal function of piglets in herds with a history of postweaning diarrhoea. All of our studies were conducted on experimental and commercial farms without a history of postweaning diarrhoea, and could therefore not be used and designed to substantiate this hypothesis [5].

In the last decades, sub-therapeutic levels of antibiotics have been included in the feed to improve

piglet performance, especially in the postweaning period. However, it was demonstrated that the use of antimicrobial growth promoters could result in bacterial resistance. The ban on in feed antibiotics by the European Union (January 2006) asks for alternatives to these antibiotics. Otherwise, the disappearance of in feed antibiotics will probably have to be substituted with an increase in the use of therapeutic antibiotics. Possible alternatives are under investigation and include the improvement of the hygiene status of farms, or the addition of alternative substances to the piglet diet, such as prebiotics. Given the beneficial effects of IS on postweaning piglet performance observed, including the diminished effect of ETEC exposure after IS with supplementary feeding [35], IS might also be considered as a strategy to reduce the use of antibiotics in pig husbandry [5].

Intermittent suckling and sow performance

Results solely focussed on the consequences of intermittent suckling regimens during an extended lactation on piglet (postweaning) performance. As mentioned previously, improving piglet postweaning performance by extending lactation length can only be profitable if reproductive performance of sows is not compromised. Hence, in addition and partly parallel to our studies, a considerable amount of research was performed investigating the effects of intermittent suckling regimens during an extended lactation on sow reproductive performance [15]. Subjecting sows to an IS regimen was found to induce lactational oestrus and ovulation in more than 80% of the sows, ultimately resulting in the establishment of the next pregnancy during the ongoing lactation period. In consecutive studies, the timing and duration of the applied IS regimens was varied. It was found that both an early onset of IS (at day 14) after parturition and a prolonged period of IS (up to 20 days after ovulation) tended to negatively affect embryo survival of the newly established pregnancy. Otherwise, the quality of lactational oestrus and of the subsequent pregnancy in sows submitted to an IS regimen was found to be rather comparable to that observed in conventionally weaned sows. Besides timing and duration of IS, some other factors, such as breed, parity, method of separation and boar contact was described [15], that might affect the number of sows responding to IS with follicle growth and ovulation. In addition, since the effect of IS on embryo survival of the next pregnancy was only studied during early pregnancy, it was stated that more insight is needed in the effects of IS regimens on the performance of the litter conceived during the extended lactation period. Finally, it was concluded that further studies taken these factors into account are necessary before implementation of IS in pig husbandry.

Future research

In this paragraph we presented several recommendations for future studies. First, suggestions are made for further studies to unravel the mechanisms behind postweaning intestinal dysfunction in pigs. Thereafter, some suggestions are made for applied research questions are formulated, investigating the benefits of IS under various farm conditions, quantification of individual preweaning feed intake, and the development of a ‘more natural’ housing system for lactating sows and their litters.

Intestinal hypoperfusion and weaning-associated villous atrophy

Postweaning villous atrophy might (partly) be caused by intestinal hypoperfusion. Severe, experimentally reduced SMA flow for 1 h was found to result in histological lesions [43]. Moreover, TPN feeding of piglets resulted in a 30% reduction of the portal and SMA blood flow after 8 h [38]. This rapid decrease in intestinal blood flow preceded the villous atrophy, suppression of cell proliferation and survival in the small intestine observed after 48 h of TPN. Since weaning is associated with a period of low feed intake or fasting, we hypothesized that splanchnic hypoperfusion might play a part in the occurrence of intestinal dysfunction after weaning.

Figure 7. Piglet with flowmeter

Figure 8. Piglet with flowmeter

Our results indicated that the Physiogear™ I wireless flowmeter can be used to measure flow in group-housed animals without any human contact [2]. It was indicated that this tool enables one to measure the SMA blood flow in weaned piglets, providing the opportunity to relate flow measurements to undisturbed animal behavior and performance [2]. Unfortunately, the experimental design and the low number of animals used in this pilot study are not appropriate to substantiate the above described hypothesis (which was evidently beyond the scope of this pilot study). Hence, more research is needed investigating whether weaning is associated with a reduced intestinal blood flow possibly (in part) responsible for the postweaning intestinal dysfunction.

A recent study [49] investigated the effect of the administration of 2-iminobiotin (2-IB; a compound with neuroprotective properties in perinatal, experimentally-induced hypoxia-ischemia conditions) at birth on piglet growth rates, morbidity and mortality under farm conditions. Piglets treated with 2-IB after birth had a higher growth rate in the first 10 days after birth and tended to at weaning compared to untreated control piglets. The authors of this study postulated that the administration of 2-IB might have ameliorated the adverse effects of hypoxia and ischemia experienced during birth on the gastrointestinal tract, ultimately resulting in the improved neonatal growth rates [49]. In future studies the Physiogear™ I wireless blood flow meter and the administration of a compound with neuroprotective properties, such as 2-IB, or a combination of both can be used to elucidate whether the postweaning small intestinal villous atrophy and dysfunction in piglets is (partly) mediated by intestinal hypoperfusion.

Plasma citrulline concentration and postweaning intestinal function

One of our aims was to investigate possible (biological) markers, which enable longitudinal monitoring of intestinal function in weaned piglets. We demonstrated that weaning is associated with a rapid reduction of the plasma citrulline concentration in piglets [6]. Moreover, a distinct correlation was found between plasma citrulline and mannitol concentrations on day 4 postweaning [6]. Yet, no (or only a weak) correlations between plasma citrulline concentrations and the intestinal morphology were found. Although there were some distinct differences in gut morphology between IS and conventional piglets after weaning, no differences in plasma citrulline concentration were found. On the one hand, the sampling location (jugular vein) might not have been adequate to detect changes in citrulline

production. Moreover, it has to be stated that this was a transverse study in which piglets were not fasted before the blood sample was obtained. This might explain the higher variation in plasma concentrations generally observed in the study [5] [6]. This increased variation might have complicated the detection of a possible relation between plasma citrulline concentrations and gut morphology. On the other hand, differences in plasma citrulline concentration might not have to be correlated to changes intestinal morphology per se, in order to consider it a marker for intestinal function. Previous studies [34] [35] [36] did not find a relationship between net absorption values of the small intestine and villous height and crypt depth after weaning. These authors suggest that the lack of a correlation could be explained by the presence of young, immature enterocytes in the intestine. Hence, further research is needed to investigate whether plasma citrulline concentration is an adequate marker of intestinal function.

Gut related hormones and weaning-associated anorexia and villous atrophy

We speculate that the absence of villous atrophy at day 2 postweaning, as prevented by applying one week of IS before weaning at day 26 [5], might have been involved in the higher feed intake levels observed between day 2 and 7 postweaning compared to conventional weaned piglets. The cells lining the small intestinal lumen are responsible for the production of quite some intestinal hormones, such as gastric inhibitory polypeptide (GIP) and glucagon-like peptide-2 (GLP-2), involved in appetite regulation. Disrupting the small intestinal integrity and function by postweaning villous atrophy, as observed in conventionally weaned piglets [5], might also have influenced the crosstalk between gut and brain via these mediators, resulting in the lower feed intake levels observed in the conventionally weaned piglets. It would be most interesting to study the effects of weaning on plasma concentrations of gut hormones and their possible involvement in postweaning anorexia.

Benefits of IS under various farm conditions

Subjecting piglets to IS during the (extended) lactation period was found to prevent the weaning-associated small intestinal villous atrophy [5]. We suggest that the beneficial effects of IS on postweaning gut characteristics reduces the risk on the development of postweaning diarrhoea. Yet, our studies were conducted on experimental and commercial farms without a history of postweaning diarrhoea. In a study [35] piglets subjected to IS with supplementary feeding during the suckling period were found to have an attenuated reduction in small intestinal absorption after ETEC exposure. Hence, we postulate that IS could improve the postweaning intestinal function in piglets of herd with a history of postweaning diarrhoea. Moreover, it might decrease the use of therapeutic antibiotics on (these) pig husbandry farms. Future studies either in herds with a history of postweaning diarrhoea or in herds experimentally infected with ETEC and/or rotaviruses might indicate whether an IS regimen can diminish the detrimental effects of weaning on piglet performance under these circumstances.

Individual preweaning feed intake and postweaning piglet performance

Preweaning creep feed intake was found to be highly variable both between litters [39] and between piglets of the same litter [9] [40]. As described [9] two mechanisms have been proposed that might explain this high variation in individual creep feed intake. First, it could be explained by maturation; piglets with a more matured gastrointestinal tract might consume more creep feed, since they are better capable to digest and absorb the nutrients from the solid feed. In several studies, a positive correlation was observed between weight and preweaning feed intake, indicating that large piglets, occupying the more productive (anterior) teats, consumed more food [40]. On the other hand, it could be explained by the need for energy intake, suggesting that piglets with an inadequate milk intake compensate for it with an increased creep feed consumption. In line with this hypothesis, piglets with the highest gain in the preweaning week, indicating a good teat quality, were found to consume less solid feed [1]. Irrespective of motivation, the high variation in creep feed intake of individual piglets complicate the investigations of the effects of preweaning creep feed on postweaning piglet performance. This becomes evident from the equivocal effects of creep feed supplementation during the lactation period on postweaning intestinal function, even when eaters and non-eaters could be recognized [9] [27]. Hence, quantification of individual creep feed intake is necessary. Moreover, the development of a method to asses individual creep feed intake of piglets would provide the opportunity to further investigate the piglet's motivation for the consumption of solid feed during the suckling period.

Figure 9. Piglet eating

Gradual adaptation to weaning

Confining sows and their litters to conventional housing conditions denies them the opportunity to a gradual weaning process. This becomes evident from the high and hardly undiminished nursing frequency at weaning and the concomitant low preweaning solid feed intake of the piglets. As mentioned before, the abrupt weaning of piglets is associated with detrimental effects on postweaning piglet performance, and even piglet death. Hence, in our opinion it is highly desirable, if not a necessity, to improve the adaptation of piglets to weaning under farm conditions. Several alternative management strategies, such as sow controlled housing combined with a communal piglet area, were found to improve piglet postweaning performance, as judged by piglet growth and feed intake, as well as behaviour. Moreover, these improvements on piglet's adaptation to weaning coincided with substantial benefits for the sow, such as leaving the litter at will and participate in a more complex social environment of the get away area. Yet, the high variation by which the contact with the litter is reduced by the sow is a disadvantage of this alternative housing. As suggested previously, combining such sow controlled housing systems with IS, would reduce the variation of litters in their response to this housing system. Moreover, given the increasing time spent away from the litter during the lactation period when contact is controlled by the sow, one might ask to what extent a more gradual increase of the separation interval (h/day) might further improve this combination of alternative housing systems. To conclude, more research is needed to investigate how alternative management strategies can attribute to the realization of a (required) more gradual transition of piglets to weaning, preferably without compromising the high levels of production achieved in conventional systems.

Figure 10. Piglets in nursery pen without sow

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