Animal 17 (2023) 100725

Contents lists available at ScienceDirect

Animal
The international journal of animal biosciences

Effect of low colostrum intake on gastrointestinal development and uterine and cervical morphometrical architecture in the neonatal gilt

P. Langendijk *, M. Fleuren, K. Venrooy, K. Ernst, G. Page

Trouw Nutrition R&D, Stationsstraat 77, 3811 MH Amersfoort, The Netherlands

A R T I C L E I N F O

Article history:
Received 25 July 2022
Revised 24 January 2023
Accepted 26 January 2023
Available online 2 February 2023

Keywords:
Endometrium
Intestine
Piglet
Postnatal
Reproduction

A B S T R A C T

To assess the importance of natural variation in colostrum intake on piglet gastrointestinal and reproductive development, two equally sized female piglets from each of 27 litters were selected, one with low (average 226 g) and one with high (average 401 g) colostrum intake. At weaning (23 d of age), piglets were euthanised to perform macromorphological measurements on ileum, colon, cervix and uterus tissues, and to obtain tissue samples from the cervix and uterus for histology. Sections of uterine and cervical preparations were analysed using digital image analysis. Despite being selected for the same birth weight (average 1.1 kg, standard deviation 0.18 kg), piglets with low colostrum intake weighed 5.91 ± 0.17 kg and piglets with high colostrum intake weighed 6.96 ± 0.19 kg at weaning ($P < 0.05$). Most of the micro- and macroscopic measures such as length and weight of ileum and colon, cervix and uterus, luminal size of cervix and uterus, number of cervical crypts and uterine glands, were greater in gilts with high colostrum intake. The histological architecture of the uterus and cervix in gilts with high colostrum intake showed more complexity, reflecting more advanced development in these piglets. In conclusion, these data demonstrate that independent of birth weight, natural variation in colostrum intake is related to the overall development of neonatal piglets, affecting body growth, as well as growth and development of the gut and reproductive tract.

Implications

Colostrum intake is important for the survival and development of the neonatal piglet. A number of studies have shown that piglets with colostrum intake below 250 g are at increased risk of dying in the first week of life. The current study adds to the importance of colostrum in that it demonstrates the effects of low colostrum intake on the growth of young piglets and on early development of their organs, such as the reproductive tract. The results suggest that early life events may have a crucial impact on later life development and function.

Introduction

The importance of colostrum intake for survival of the neonate piglet has been illustrated in observational studies and is evident from the exponential increase in neonatal mortality when colostrum intake drops below 250 g (Ferrari et al., 2014; Devillers et al., 2011). Since colostrum intake is strongly related to birth weight (Theil et al., 2014; Devillers et al., 2011), the importance of colostrum to survival may be confounded with the impact of birth weight. Nevertheless, it is evident that immunoglobulins and other proteins in colostrum, as well as lactose and fat, provide essential support for thermoregulation and passive immunity, and that the amount of colostrum intake has a lasting effect on circulating immunoglobulins in the piglet and on growth up to the point of weaning and beyond (Devillers et al., 2011).

Apart from macro-factors such as fat, lactose, protein and immunoglobulins, colostrum contains a myriad of growth and endocrine factors, microminerals, and vitamins, such as IGF-1, insulin, vitamin D, and lactoferrin (reviewed by Hurley, 2015). The role of these factors, however, has scarcely been investigated. For example, neonate piglets are deficient in vitamin D by standards for mature pigs (Goff et al., 1984; Coffey et al., 2012). The role of colostrum in supplementing vitamin D remains unclear, although it may be significant, since the prenatal placental transfer of vitamin D to the foetus is limited (Matte and Audet, 2020). Experimental interventions (Camp et al., 2014; Ho et al., 2017), where female piglets were denied colostrum after birth and fed a milk replacer instead, have demonstrated that colostrum stimulates glandular development in the luminal epithelium of the uterus and the cervix in two-week old gilts. Supplementing IGF-1

* Corresponding author.
E-mail address: pieter.langendijk@trouwnutrition.com (P. Langendijk).

https://doi.org/10.1016/j.animal.2023.100725
1751-7311/

in colostrum-deprived piglets seems to compensate some of the observed effects, and from a review by Bagnella and Bartol (2019), pro-relaxin is another colostrum-borne factor that plays a role in early reproductive tissue development.

Complete denial of colostrum to neonate piglets may clearly affect development in experimental studies; however, it is not clear how normal variation in colostrum intake contributes to variation in the development of neonate piglets. Moreover, in most studies, low colostrum intake is confounded with low birth weight and may well be a reflection of the condition of a piglet at birth, rather than the reason for compromised development, or even mortality. This study therefore was designed to assess the effects of normal variation in colostrum intake on the development of reproductive tract tissues in gilts with similar birth weight and condition at farrowing.

Material and methods

Animal procedures

Experimental work and procedures were approved by the Central Commission for Animal Experiments, The Hague, The Netherlands, (approval number AVD2040020173225) and were in compliance with EU Directive 2010/63/EU. Piglets used in this study were born to mixed parity F1 sows (Hypor Libra, Hendrix Genetics, Boxmeer, The Netherlands). Average number of piglets born alive was 15.1, and the litter size at weaning was 13.1. The sows used for this study were allowed to farrow spontaneously without induction, manual assistance or injections with oxytocin. Sows were housed in standard commercial farrowing crates with feeding trough and drinker, on slats. A creep area with heating lights was provided to the piglets for the first week after farrowing. Temperature in the farrowing room was kept constant at 23–24 °C. From seven days prior to farrowing, sows were fed 3.0 kg per day of a typical commercial lactation diet (2137 kCal/kg, 9.1 g/kg SID Lys). Sows had ad libitum access to water. Once sows had farrowed (d0), feed allowance was increased by 0.5 kg/d each day from d1, until the maximum allowance was reached. Lights were on from 0600 a.m. until 1000 p.m. Piglets did not have access to creep feed.

From 27 litters, pairs of female piglets with similar birth weights were selected, one with low colostrum intake (<250 g) and one with high colostrum intake (>300 g). Colostrum intake per piglet was estimated based on birth weight taken immediately at birth, and 24 h later, according to the equation developed by Theil et al. (2014): Colostrum intake (g) = −106 + 2.26WG + 200 BWB + 0.111D – 1414WG/D + 0.0182WG/BWB. **WG** = weight gain between birth and 24 h (g), **BWB** = birth weight (kg), and **D** = interval between the first weight and the second weight (min). Care was taken to select pairs with birth weights as close as possible (average 1.1 kg for both groups, standard deviation 0.2 and 0.1 kg for low and high colostrum, respectively).

Sample preparation

At weaning (average 23 d of age), the selected pairs of gilts were weighed and euthanised by intravenous injection of pentobarbital (Euthasol, AST Farma, Oudewater, Netherlands) into the jugular vein, and subsequently exsanguinated. The reproductive tract (uterus and ovaries) was excised and after taking macroscopic measures, one uterine horn and the cervix were stored in 4.0% formaldehyde until the preparation of slides for histology. The cervix was defined as running from the bifurcation of the two horns to the point where the urethra connected to the cervix/vagina and therefore included half of the uterine body and the cranial vagina. In addition, the length and weight of ileum and colon were measured. Histology samples were prepared by the National Animal Health Centre (GD, Deventer, The Netherlands). For the preparation of histology samples, a 1 cm section of the middle of the cervix and uterus was dissected and divided into three parts of 3–5 mm thickness and embedded in paraffin wax. From this sample, sections of 2 μm were mounted on slides and stained with hematoxylin/eosin. These sections were used for histological measurements on the morphometric architecture of the uterine and cervical lumen and glands as described by Camp et al. (2014) and Miller et al. (2012), and illustrated in Fig. 1. Histomorphometric measurements on one complete section of the cervix and one complete section of the uterus per piglet were obtained using an inverted microscope (Nikon Eclipse Ti2) with a mounted digital camera, using the NIS-D software.

Statistical analysis

Statistical analyses of the data were carried out in SAS (SAS Studio, SAS Institute Inc., Cary, NC, USA). Level of significance was set at $P < 0.05$, and a tendency was considered at $0.05 \leq P \leq 0.10$. Normality of the measures was checked using the UNIVARIATE procedure using the Shapiro-Wilk test. Both the cervical and uterine surfaces of the lumen were transformed with a square root transformation. All microscopic and macroscopic measures were analysed with the MIXED procedure. The model included sow as random factor and piglets nested within sow, colostrum intake (low and high) as a fixed factor, and BW at dissection as a covariate. Pearson correlations were used to assess the relationships amongst various measures.

Fig. 1. Description of histomorphometric measures in cervix (A) and uterine horn sections (B), in tissue samples taken from 23 d old piglets. LE: luminal epithelium, myo: myometrium, Crypt 1: primary crypt, Crypt 2: secondary crypt. 20× magnification.

Results

All selected piglets survived to weaning. Average colostrum intake in the population where the piglets were selected from was 380 g, but varied considerably, with a standard deviation of 269 g. In the overall population, 23% of the piglets consumed less than 250 g of colostrum. Average colostrum intake was 226 ± 45 g in the piglets selected for low intake (**L**) and 401 ± 77 g in the piglets selected for high intake (**H**). In the 27 selected pairs of piglets, the average birth weight was 1.09 kg (standard deviation 0.18 kg). Piglets with low colostrum intake weighed 1.06 ± 0.22 kg, and piglets with high colostrum intake weighed 1.13 ± 0.13 kg on average at birth ($P < 0.05$). The difference in birth weights between the two piglets within a pair was always between 0 and 360 g. Birth weight was considered in the statistical model, but did not affect any of the differences between low and high colostrum intake piglets ($P > 0.10$). Birth order (median 8) was similar for the two groups of piglets.

At weaning, piglets with low colostrum intake weighed 5.91 ± 0.17 kg and piglets with high colostrum intake weighed 6.96 ± 0.19 kg ($P < 0.05$), the difference being independent of birth weight (Fig. 2). Macroscopic measures of the gut (length and weight of ileum and colon) at 25 d of age were 9–15% greater for piglets with high colostrum intake (Table 1). Similarly, most of the macroscopic measures on the reproductive tract (uterus and cervix) were greater or tended to be greater for piglets with high colostrum intake. Most of the micro- and macroscopic measures such as length and weight of ileum and colon, cervix and uterus, luminal size of cervix and uterus, number of cervical crypts and uterine glands were greater in gilts with high colostrum intake (Table 1). The complexity of the uterine stroma and luminal epithelium, as reflected by the number of endometrial glands and the size of the lumen, was more developed in piglets with high colostrum intake. The number of glands, for example, tended to be increased by 25% ($P < 0.09$) in piglets with high colostrum intake. Similarly, complexity in the cervical structure was more developed in the piglets with high colostrum intake. The size of the cervical lumen was increased by 40% ($P < 0.01$), and the number of secondary crypts, which branch off the primary crypts, was increased by 28% ($P < 0.05$).

When piglet weight at the time of dissection was included as a covariate in the statistical model, most of the differences in microscopic and macroscopic measures were no longer significant, suggesting that to some extent, the differences between the two groups were confounded with size of the piglets. There were some exceptions to this though. The thickness of the stroma in both uterus and cervix sections, the luminal surface area, and the length of the uterine horns were more significant, or remained significantly different between the two groups, when weight was included as a covariate. The various measures presented in Table 1 were correlated with BW. Macroscopic measures of the gut and the cervix and uterus had a correlation coefficient (r) between 0.4 and 0.7 with BW ($P < 0.05$). The correlation between microscopic measures and BW varied between 0.2 and 0.4 ($P < 0.05$), and for some measures was not significant.

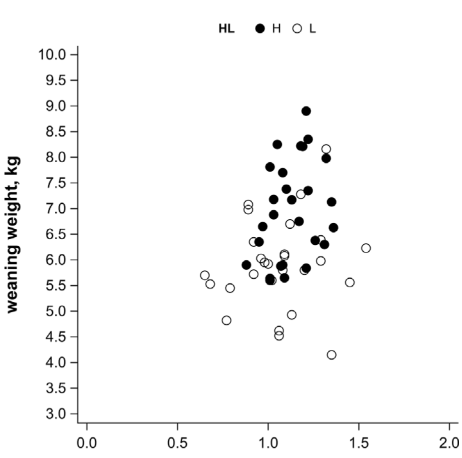

Fig. 2. Weight at 25 d of age for piglets with low (L) or high (H) colostrum intake, but similar birth weight (around 1.1 kg).

Discussion

The pairs of gilts selected in this study had similar birth weights (1.06 and 1.13 kg for low and high colostrum intake) and within each pair birth weights were within 360 g of each other. In addition, the birth order was similar for piglets with high colostrum intake and piglets with low colostrum intake, which suggests that the condition in terms of impact of the farrowing process and oxygenation status was similar. Langendijk et al. (2018) demonstrated that the later piglets are born in a litter, the higher the risk of asphyxiation, increased blood lactate, reduced blood pH, and increased effects on neonatal performance such as colostrum intake and survival. The effects in this study therefore can be ascribed to the difference in colostrum intake and not to birth weight or birth order. Furthermore, the pairs of (high and low colostrum intake) piglets were selected from the same dam and not cross-fostered, to ensure a similar maternal environment throughout the rest of lactation.

Colostrum intake is critical to survive the first weeks of life. A number of studies (Ferrari et al., 2014; Devillers et al., 2011) have shown that neonatal survival increases with increasing colostrum intake. The energy requirements for maintenance and thermoregulation exceed the fat and glycogen reserves at birth, and therefore, fat and protein in colostrum are essential to prevent hypothermia and starvation (Le Dividich et al., 2005). Since the neonate piglet is immunologically immature, colostrum-borne immunoglobulins provide the first protection against pathogens, and help the piglet to counteract pathogens that may otherwise cause diarrhoea and mortality. Interestingly, Devillers et al. (2011) not only demonstrated the importance of colostrum intake for Immunoglobulin G (**IgG**) levels in the neonate pig but also found that IgG levels at 24 h after birth were strongly related to circulating IgG at the time of weaning. The authors suggested that some of the immunoglobulins at weaning were remnants of those consumed with colostrum at birth. However, given the half-life of immunoglobulins, at least part of the IgG at weaning would have resulted from the activation of the piglets' own immune system. Apart from direct protection of the neonate against pathogens, colostrum-borne IgG's may contribute to longer-term effects on development (Devillers et al., 2011). Although some of these effects are likely confounded with birth weight, the above observations underline the importance of colostrum-borne factors for the development of piglets. The current study confirms the relevance of colostrum intake for piglet weight gain through lactation, independent of birth weight, since piglets with high colostrum intake (average 401 vs 226 g) were around 1 kg heavier at weaning (7 vs 6 kg), despite having similar birth weights (1.13 vs 1.06 kg).

Other than fat, lactose, protein and immunoglobulins, colostrum contains a host of factors such as growth factors, cytokines, vitamins, endocrine factors, and microminerals (Hurley, 2015). The relevance of these factors has been less well researched. Complete denial of colostrum in the first 24 h of life is clearly detrimental to piglet growth and development of the gastrointestinal tract and organs (Widdowson and Crabb, 1976; Widdowson et al.,

Table 1
Morphometric measures of uterine and cervix sections, and of ileum and colon at 25 d of age, in gilts with low or high colostrum intake.

Variable	Low colostrum intake (n = 27) Mean ± SE	High colostrum intake (n = 27) Mean ± SE	*P*-value[1]	*P*-value with BW as covariate[1]
Birth weight, kg	1.06 ± 0.04	1.13 ± 0.02	0.05	–
Birth order, n	7.5 ± 0.7	7.9 ± 0.9	0.68	–
BW at weaning (kg)	5.91 ± 0.17	6.96 ± 0.19	<0.001	–
Weaning age, d	22.6 ± 0.3	22.7 ± 0.3	0.16	–
Colostrum intake (g)	226 ± 9	401 ± 15	<0.001	–
Cervix				
Length, cm	5.18 ± 0.25	5.53 ± 0.15	0.09	0.58
Weight, g	0.62 ± 0.02	0.68 ± 0.02	0.05	0.66
Diameter lumen, mm	0.99 ± 0.06	1.24 ± 0.06	0.01	0.01
Surface lumen, mm^2	0.87 ± 0.07	1.41 ± 0.17	0.01	0.04
Luminal epithelium thickness, µm	24.61 ± 0.71	23.98 ± 0.61	0.48	0.91
# Crypt 1, n	16.74 ± 0.69	18.85 ± 1.17	0.14	0.35
# Crypt 2, n	9.56 ± 1.05	12.22 ± 1.24	0.05	0.13
Total crypt length, mm	7.0 ± 0.54	8.42 ± 0.65	0.10	0.84
Stroma thickness, mm	1.65 ± 0.10	1.82 ± 0.12	0.27	0.11
Uterus				
Length (cm)	9.88 ± 0.22	9.95 ± 0.22	0.79	0.06
Weight (g)	0.62 ± 0.03	0.70 ± 0.03	0.02	0.30
Surface lumen, mm^2	0.36 ± 0.05	0.50 ± 0.07	0.11	0.37
Circumference lumen, mm	4.74 ± 0.18	5.52 ± 0.23	<0.01	0.15
Luminal epithelium thickness, µm	28.82 ± 0.69	27.38 ± 0.63	0.16	0.37
Stroma thickness, mm	0.65 ± 0.03	0.64 ± 0.02	0.89	0.11
Myometrium thickness, mm	0.21 ± 0.006	0.21 ± 0.01	0.53	0.53
# Glands, n	33.15 ± 4.06	41.74 ± 4.20	0.09	0.90
Total gland surface, mm^2	0.020 ± 0.004	0.020 ± 0.003	0.46	0.53
Gut				
Length ileum, m	7.5 ± 0.2	8.2 ± 0.2	<0.01	0.17
Weight ileum, g	199 ± 8	219 ± 8	0.06	0.8
Length colon, m	1.33 ± 0.04	1.45 ± 0.03	0.04	0.5
Weight colon, g	46.9 ± 2.1	53.9 ± 1.8	0.03	0.9

[1] *P*-values are given for the difference between piglets with high and low colostrum intake. In the left column are *P*-values not taking BW into account; in the right column are *P*-values when BW at euthanisation was included as a covariate.

1976; Zhang et al., 1998). Feeding milk replacer instead of colostrum does restore most of the growth and development in fasted piglets (Burrin et al., 1995), indicating that some of this growth is nutrient dependent. However, colostrum has additional effects beyond milk replacer, indicating that non-nutritive factors present in colostrum but not in milk are responsible for stimulating gastrointestinal tract development, and the development of muscle and organs (Burrin et al., 1995; Fiorotto et al., 2000). Insulin-like growth factor 1 (**IGF-1**) was indicated to be responsible for some of these non-nutritive effects of colostrum, since oral supplementation partially restored the impacts of colostrum deprivation on gastrointestinal tract development (Burrin et al., 1995). Similar effects of IGF-1 on the development of reproductive tract tissue (uterus and cervix) were demonstrated by Camp et al. (2014), indicating that IGF-1 does enter the circulation at least in the first 24 h of life and has specific roles in systemic development. These are examples of the few bioactive components that have been studied. Obviously, there are potentially many other factors such as epidermal growth factors, lactoferrin, and exosomes that influence neonatal development.

The above experimental models were all based on complete deprivation of colostrum. The current paper explored the significance of natural variation in the development of uterine and cervical morphometric aspects. Our results suggest that poor intake of colostrum may compromise development of the gastrointestinal and reproductive tracts. Our results also show that natural variation in colostrum intake is at least partially related to overall weight gain. The effects of colostrum on uterine and cervical developmental aspects were associated with overall BW, and therefore, the effects may be related to the overall maturation of the piglet. Which factors in colostrum contribute to the presented effects remains unclear, but based on previously referenced studies, IGF-1 is probably-one of the key factors.

It is interesting to speculate how the effects of colostrum at this young age may affect the reproductive performance of gilts later in life. Although the gilts in the current study were not followed after weaning, other studies on the effects of gilts' history on their subsequent reproductive performance in the breeding herd do shed some light on this aspect. Gilt progeny for example are known to perform less well in later life than sow progeny in terms of growth, and this is believed to be related to birth weight of the progeny and quality of the dam's colostrum (Miller et al., 2012). Gilt progeny were also later in achieving puberty, although once selected for breeding, they did not necessarily have smaller litters than sow progeny (Craig et al., 2017). In a review on determinants of gilt performance, Flowers (2015) presented data to show that female piglets that were reared in larger litters had lower ovulation rates, reduced embryo survival, and reduced litter size as a breeding sow. Piglets reared in larger litters would experience more competition for colostrum and milk and therefore be reared in less favourable maternal conditions. More specifically, Vallet et al. (2015) reported a relationship between colostrum intake, and age at puberty, and litter size in subsequent parities. The above examples do suggest that the effects of colostrum intake on the early development of gilt piglets reported in this paper may have long-term consequences for reproductive performance as a sow.

Conclusion

In conclusion, this paper demonstrates birth weight-independent effects of poor colostrum intake on the growth of neonatal piglets and development of the gastrointestinal and reproductive tract at 23 d of age. How the effects of low colostrum impact on later life reproductive performance and longevity need to be investigated; however, these results clearly emphasise the need for colostrum-enhancing strategies.

Ethics approval

Experimental work and procedures were approved by the Central Commission for Animal Experiments, The Hague, The Netherlands, (approval number AVD2040020173225) and were in compliance with EU Directive 2010/63/EU.

Data and model availability statement

The data/models were not deposited in an official repository. The data/models that support the study findings are available from the authors upon request.

Author ORCIDs

Pieter Langendijk: https://orcid.org/0000-0001-5055-363X.
Greg Page: https://orcid.org/0000-0001-8280-9847.

Author contributions

P. Langendijk designed the study and was the main author of the paper. **M. Fleuren** and **K. Venrooy** were in charge of coordinating the study, collection and processing of data, and data analysis. **K. Ernst** performed image analysis on histological preparations and histology data analysis. **G. Page** contributed to the data interpretation and writing of the paper.

Declaration of interest

Authors declare no conflict of interest.

Acknowledgements

None.

Financial support statement

This research received no specific grant from any funding agency, commercial or not-for-profit section.

References

Bagnella, C.A., Bartol, F.F., 2019. Relaxin and the 'Milky Way': The lactocrine hypothesis and maternal programming of development. Molecular and Cellular Endocrinology 487, 18–23.

Burrin, D.G., Davis, T.A., Ebner, S., Schoknecht, P.A., Fiorotto, M.L., Reeds, P.J., McAvoy, S., 1995. Nutrient-independent and nutrient-dependent factors stimulate protein synthesis in colostrum-fed newborn pigs. Pediatric Research 37, 593–599.

Camp, M.E., Wiley, A.A., Boulos, M.B., Rahman, K.M., Bartol, F.F., Bagnell, C.A., 2014. Effects of age, nursing, and oral IGF1 supplementation on neonatal porcine cervical development. Reproduction 148, 441–451.

Coffey, J.D., Hines, E.A., Starkey, J.D., Starkey, C.W., Chung, T.K., 2012. Feeding 25-hydroxycholecalciferol improves gilt reproductive performance and fetal vitamin D status. Journal of Animal Science 90, 3783–3788.

Craig, J.R., Collins, C.L., Athorn, R.Z.A., Dunshea, F.R., Pluske, J.R., 2017. Investigating the reproductive performance of gilt progeny entering the breeding herd. Journal of Swine Health and Production 25, 230–237.

Devillers, N., Le Dividich, J., Prunier, A., 2011. Influence of colostrum intake on piglet survival and immunity. Animal 5, 1605–1612.

Ferrari, C.V., Sbardella, P.E., Bernardi, M.L., Coutinho, M.L., Vaz Jr, I.S., Wentz, I., Bortolozzo, F.P., 2014. Effect of birth weight and colostrum intake on mortality and performance of piglets after cross-fostering in sows of different parities. Preventive Veterinary Medicine 114, 259–266.

Fiorotto, M.L., Davis, T.A., Reeds, P.J., Burrin, D.G., 2000. Nonnutritive factors in colostrum enhance myofibrillar protein synthesis in the newborn pig. Pediatric Research 48, 511–517.

Flowers, W.L., 2015. Litter-of-origin traits and their association with lifetime productivity in sows and boars. Molecular Reproduction and Development 2022, 1–9. https://doi.org/10.1002/mrd.23565.

Goff, J.P., Horst, R.L., Littledike, E.T., 1984. Effect of sow vitamin D status at parturition on the vitamin D status of neonatal piglets. Journal of Nutrition 114, 163–169.

Ho, T.Y., Rahman, K.M., Camp, M.E., Wiley, A.A., Bartol, F.F., Bagnell, C.A., 2017. Timing and duration of nursing from birth affect neonatal porcine uterine matrix metalloproteinase 9 and tissue inhibitor of metalloproteinase 1. Domestic Animal Endocrinology 59, 1–10.

Hurley, W.L., 2015. Composition of sow colostrum and milk. In: The gestating and lactating sow. Editor: Farmer, C. Wageningen Academic Publishers, Wageningen, Netherlands, pp. 193-229.

Langendijk, P., Fleuren, M., van Hees, H., van Kempen, T., 2018. The course of parturition affects piglet condition at birth and survival and growth through the nursery phase. Animals 8, 60. https://doi.org/10.3390/ani8050060.

Le Dividich, J., Rooke, J.A., Herpin, P., 2005. Nutritional and immunological importance of colostrum for the new-born pig. Journal of Agricultural Science 143, 469–485.

Matte, J.J., Audet, I., 2020. Maternal perinatal transfer of vitamins and trace elements to piglets. Animal 14, 31–38. https://doi.org/10.1017/S175173111900140X.

Miller, Y.J., Collins, A.M., Smits, R.J., Thomson, P.C., Holyoake, P.K., 2012. Providing supplemental milk to piglets preweaning improves the growth but not survival of gilt progeny compared with sow progeny. Journal of Animal Science 90, 5078–5085.

Theil, P.K., Flummer, C., Hurley, W.L., Kristensen, N.B., Labouriau, R.L., Sørensen, M.T., 2014. Mechanistic model to predict colostrum intake based on deuterium oxide dilution technique data and impact of gestation and prefarrowing diets on piglet intake and sow yield of colostrum. Journal of Animal Science 92, 5507–5519.

Vallet, J.L., Miles, J.R., Rempel, L.R., Nonneman, D.J., Lents, C.A., 2015. Relationships between day one piglet serum immunoglobulin immunocrit and subsequent growth, puberty attainment, litter size, and lactation performance. Journal of Animal Science 93, 2722–2729. https://doi.org/10.2527/jas2014-8535.

Widdowson, E.M., Crabb, D.E., 1976. Changes in the organs of pigs in response to feeding for the first 24h after birth. I. The internal organs and muscle. Biology of the Neonate 28, 261–271.

Widdowson, E.M., Colombo, V.E., Artavanis, C.A., 1976. Changes in the organs of pigs in response to feeding for the first 24h after birth. II. The digestive tract. Biology of the Neonate 28, 272–281.

Zhang, H., Malo, C., Boyle, C.R., Buddington, R.K., 1998. Diet influences development of the pig (sus scrofa) intestine during the first 6 hours after birth. Journal of Nutrition 128, 1302–1310.