Perspectives

Lactation in swine: review article

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Implications

- Mammogenesis and first lactation performance are key for lifelong milk production in the sow.
- Nursing behavior in pigs is complex and several interactions between the sow and her piglets are needed for a successful lactation.
- Piglet vitality is crucial for an adequate lactation performance.
- Postpartum dysgalactia syndrome is the major puerperal disease in sows and causes reduced animal health and welfare, leading to economic losses in a sow herd.

Key words: colostrum, mammary gland, sow, postpartum dysgalactia syndrome, vitality

Introduction

The development of the mammary gland and milk production in sows are important factors for health and productivity but also for adequate development of the offspring. Sow nutrition and catabolism (Einarsson and Rojkittikhun, 1993), hormonal status (Varley and Foxcroft, 1990; Farmer, 2022), pharmacology (Farmer, 2016), genetics and environment/climate (Rydhmer, 2000; Yun and Valros, 2015; Bjerg et al., 2020) all have substantial effects on the development and health of the mammary gland in sows but have been reviewed previously and so will receive little attention here. This review should give a brief overview on lactation in swine, focusing on the coordinated interplay between behavior and physiology of the sow and her litter. In addition, postpartum dysgalactia syndrome (PPDS) will be described with a focus on recent diagnostic measures of the mammary gland for disease surveillance and as indicators for sow productivity.

Sow Related Factors

Development of the mammary gland

Mammogenesis is a continuous process and therefore several parameters are involved to obtain an adult mammary gland with optimal function in sows. The most important structural elements of the mammary gland are formed in the fetal stadium before the piglet is born (Hurley, 2019). In the prepubertal phase, the mammary gland parenchyma grows slowly until 90 days of age. Due to an increase of circulating oestrogen, the weight of the mammary gland almost quadruples after this point (Hurley, 2019). Ad libitum feeding during this period increases mammary parenchymal weight by 36% to 52% compared with a 20% to 25% feed restriction (Farmer, 2018). After puberty, cyclic gilts have more parenchymal mammary gland tissue than noncyclic gilts (Farmer, 2018). The mammary gland does not enlarge in the first two thirds of gestation (Sørensen et al., 2002). However, in the last third of gestation, the parenchyma of the mammary gland increases by up to 200%, and at the same time, the fat content decreases by almost 70%. This decrease in adipocytes and increase in epithelial structures is due to the formation of the alveoli. In addition, the extra-parenchymal tissue enlarges by up to 170% (Weldon et al., 1991; Sørensen et al., 2002). The middle glands (glands 3, 4, and 5) usually reach the largest tissue mass, followed by the two anterior mammary glands (glands 1 and 2) (Ji et al., 2006). From day 105 of gestation, the epithelial cells begin to differentiate with an increase in intracellular content of milk droplets and formation of the typical polarity of secretory tissue to start lactogenesis. This development is completed around day four of lactation (Hurley, 2019). Before and after farrowing, the hormones progesterone, estrogen, prolactin, and relaxin are involved in the peripartal formation of the mammary gland, whereby relaxin and prolactin have the most important effect (Hurley, 2019).

An induced hypoprolactinemia between days 90 and 110 of pregnancy in gilts leads to significantly reduced mammary parenchymal weight, total DNA, total RNA, and protein percentage (Farmer and Petitclerc, 2003; Farmer, 2022). A similar effect can be observed with relaxin, whereby ovariectomy of gilts on either day 80 or 100 of gestation leads to a drastic inhibition of mammary parenchymal tissue

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development (Hurley et al., 1991). Yet, after farrowing, the lack of relaxin incurred during gestation is mostly compensated by rapid postpartum mammary growth (Hurley, 2001). Certain plant extracts with estrogenic or hyperprolactinemic properties fed during specific time periods of mammogenesis may have a stimulating effect on mammary development. However, an optimal and valid nutritional strategy has not yet been described (Farmer, 2018). The body condition of gilts also influences mammogenesis (Farmer, 2018). The total amount of mammary parenchyma that is present at the end of gestation is crucial for future milk yield potential. Gilts that are too thin at the end of gestation (12–15 mm backfat) show impaired mammary development in comparison to gilts with greater backfat (16–26 mm) (Farmer et al., 2016b). On the other hand, gilts that are leaner (12–15 mm backfat) at mating and maintain their lean body condition throughout gestation display similar parenchymal tissue mass in late gestation than gilts with a greater backfat at mating (16–26 mm backfat) that was maintained throughout gestation(Farmer et al., 2016a). Backfat thickness in late pregnancy must therefore be considered to achieve optimal sow lactation performance (Farmer et al., 2016b).

Nursing behavior of the sow

After the rapid mammary growth that takes place in late gestation, and the endocrine activation of lactation at farrowing, there is a complex relationship between the sow and the piglets that determines the supply and maintenance of milk production for litter growth (Farmer, 2019). This differs between the colostral period and later lactation (Špinka and Illmann, 2015; Farmer, 2019). In comparison to other species, pigs have a higher nursing frequency, a shorter milk ejection, a regular occurrence of nonproductive nursings, a potential for allo-suckling, and a structured tactile and vocal communication between the sow and the piglets (Fraser, 1980). In the beginning of the colostral phase, the sow continuously exposes the udder to piglets and colostrum is always available. Therefore, the piglets can harvest colostrum by moving from teat to teat (Devillers et al., 2007; Quesnel et al., 2011). Gradually, milk ejections become dependent on tactile stimulation by the piglets (Fraser, 1980). A typical structure of nursing is established, which includes five main phases: nursing initiation, pre-ejection, milk ejection, postejection, and nursing termination (Figure 1) (Fraser, 1980). The nursing interval gets longer as lactation advances, and is on average every 50 min at the end of lactation with a wide range between individuals (Špinka and Illmann, 2015). Nursings in early lactation are most often initiated by the sow and in later lactation by the piglets and are followed by pre-ejection teat massage of the piglets (Špinka and Illmann, 2015). The massage of the udder leads to a surge of oxytocin and causes the milk ejection phase, which lasts only around 20 seconds. After milk ejection, the piglets continue with postejection massage until the nursing event is terminated by the sow or piglets (Fraser, 1980; Špinka and Illmann, 2015). Peak milk yield occurs at approximately three weeks postpartum with a mean about 10.0 kg·d^{-1} (Min 3.5 and Max 16.5) (Hansen et al., 2012).

Piglet Related Factors

Piglet vitality

Piglet factors that influence sow lactation are apparent immediately after birth. Vitality is a key determinant for feeding success in the piglet and can be affected by numerous factors, with the two greatest being birth weight and birth trauma-induced hypoxia (Alexopoulos et al., 2018; Langendijk and Plush, 2019). Light weight piglets (<1.1 kg) and those with evidence of hypoxia at birth (meconium staining) show reduced colostrum intake in the first 24 hours (Plush et al., 2018). Hypothermic piglets, as measured by low rectal temperature (<38 °C) after birth, also have reduced colostrum intake (Figure 2) (Alexopoulos et al., 2018). These three components of vitality (birth weight, hypoxia, and thermoregulatory ability) are not independent of one another. Birth weight can influence susceptibility to hypoxia, which in turn can impair thermoregulation, and birth weight-driven changes in surface area to volume ratio affect hypothermia (Kammersgaard et al., 2011). Piglet vitality is becoming an increasingly important issue in hyper-prolific sows that give birth to larger litter sizes (>16 piglets), with lighter piglets, and longer farrowing durations (Ward et al., 2020). Genetic, nutritional, and management strategies should maximize piglet vitality to ensure lactation performance.

Figure 1. Structured nursing behavior in pigs.

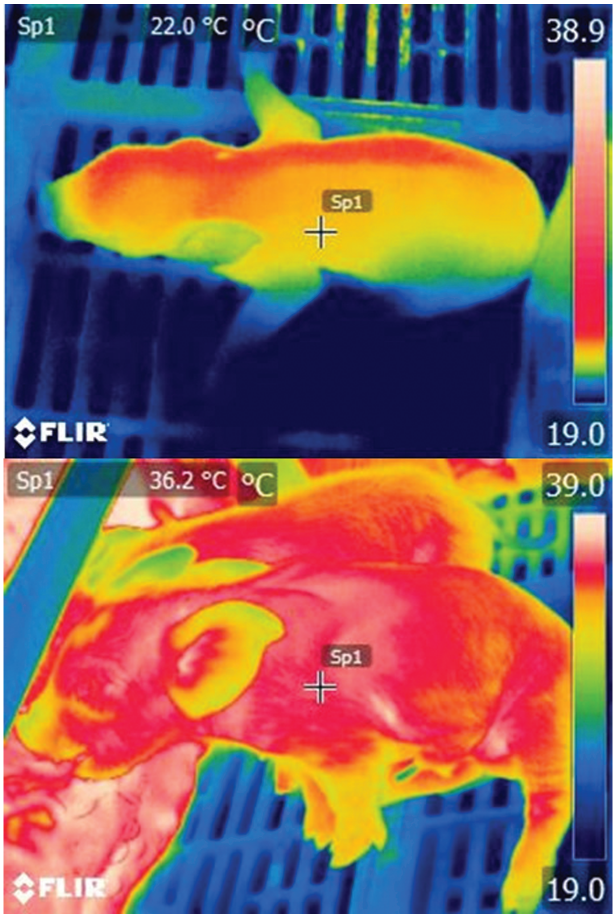

Figure 2. Thermal image detecting skin temperature of newborn piglets that are receiving colostrum (lower: 36.3 °C), and of a "low viability" piglet who has failed to reach the udder and so ingest colostrum (upper: 22.0 °C). Thermal color scale (19–39 °C) presented on the right hand-side of each image (Alexopoulos et al., 2018).

Mammary gland activation

The reason why piglet vitality is so crucial for a successful sow lactation is because of the phenomenon of teat activation. Teat activation is essential for the maintenance of milk production. Greater teat stimulation immediately after birth, driven by a larger litter size born, has been suggested as a mechanism for improved piglet growth and hence, sow milk production (Plush et al., 2019). Regular stimulation of each gland during the first 24 h post-partum results in increased milk yield when compared to glands that have not been stimulated (Theil et al., 2005). Stimulation of the gland by the piglet needs to occur for longer than twelve hours, and if left un-suckled for a period of three days, irreversible involution will take place (Theil et al., 2005). Importantly, it has been shown that unsuckled teats of primiparous sows will produce less milk and have lesser development in the subsequent lactation (Farmer, 2013). Piglets reared on second parity sows from teats not nursed in the first lactation were 0.2 kg lighter on day 7 of lactation and 1.1 kg lighter on day 56. This negative effect can be explained by a reduction in mammary parenchymal cell number and metabolic activity. Teats should be suckled for at least 48 h in the first lactation to avoid negative effects on the subsequent lactation (Farmer, 2019). What is not known is whether similar inter-parity effects are observed for multiparous sows.

Fostering and teat fidelity

After teat activation, piglets are cross-fostered as litter size does not generally align with the rearing capacity of the sow (Alexopoulos et al., 2018). However, due to the current litter sizes of hyper-prolific sows, it is not always possible to do so, because many times all sows have supernumerary piglets and therefore, other measures must be implemented on farm. Fostering, ensures that all piglets have access to a functional gland during the milk let-down event and given the lifelong impacts on suckled glands for milk production, every teat should receive a strong and healthy piglet. When the number of piglets exceeds the number of available glands, more fighting and lower suckling success is observed (Kobek-Kjeldager et al., 2020). After this fostering event, piglets develop teat fidelity. This is because the short duration of milk ejection leaves little time for piglets to fight with littermates for teat access. A stable teat order is established four days after farrowing (1st day: 5–15% of piglets have a stable teat order; 4th day: 85–95% of piglets have a stable teat order) (Puppe and Tuchscherer, 1999). The stability of this teat order was recently questioned because when litters were fostered to achieve either 14 or 17 piglets, an increase in piglet disputes at the udder was observed as lactation progressed (Kobek-Kjeldager et al., 2020). Perhaps increased sow prolificacy has challenged this innate, evolutionary adaptation in piglet behavior. Regardless, continual movement or fostering as piglets age is not advised as it results in more fighting at the udder, shorter milk let-down events, lower milk production, and poorer piglet growth (Alexopoulos et al., 2018).

Feeding behaviors

As already described, there are three specific stages during milk let-down of sows; pre let-down massage, milk ejection, and post let-down massage (Figure 1). Algers et al. (1991) have demonstrated that there is a quantitative relationship between the time teats are stimulated by piglets and prolactin concentrations, thus the piglet plays an integral factor in milk production of the sow. Udder stimulation is required to trigger oxytocin release and so milk let-down in the sow, but its release is not dependent on premassage duration or number of piglets present (Algers et al., 1990). Post let-down massage does impact on milk production (Jensen et al., 1998), a phenomenon known as the "restaurant hypothesis", with the piglet ordering the size of its next meal. Initial investigations correlated amount of litter massage with total milk input (Špinka and Algers, 1995), but later work has suggested that this relationship is between the individual gland and piglet (Jensen et al., 1998). The post let-down massage by a piglet acts to increase local blood flow and therefore nutrients and lactogenic hormones. Outside of the pre and post massaging events, ability for the piglet to drain

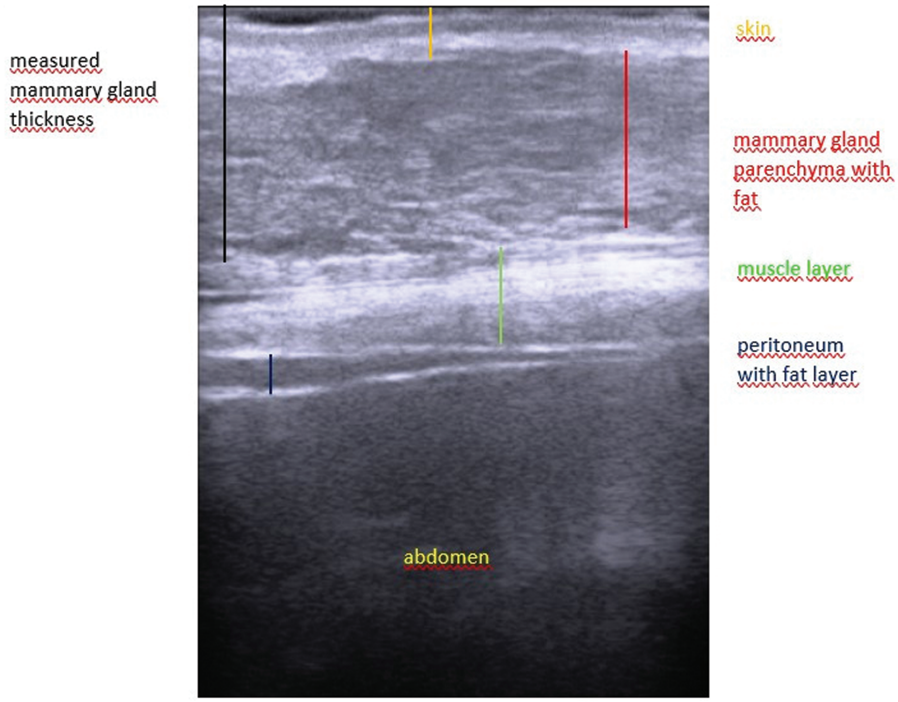

Figure 3. Ultrasound image of one mammary gland complex of a sow in the 8th parity describing the different layers of the tissue (Leuenberger and Grahofer, 2022, unpublished results).

the gland of milk completely at let-down is the key driver of milk secretion. When a gland is not drained, milk presence in mammary epithelial cells changes autocrine and endocrine factors as well as pressure acting to reduce milk production for the subsequent nursing (Hurley, 2001). To this effect, larger, aggressive piglets are more effective at emptying a gland and therefore aid in driving milk production than their smaller counterparts. Aggressive litters that demand feeding more frequently from the sow and so reduce the feeding interval seems to drive milk production (Auldist et al., 2000).

Lactation failure

Recently, lactation failure in sows has been identified as having significant, negative consequences for sow retention rates (culling for poor mothering ability, bad udder, no milk, mastitis) (Vargovic et al., 2022). Most of these criteria fit the postpartum dysgalactia syndrome (PPDS), which is the major puerperal disease in sows. The PPDS affects both the sow and her litter and, therefore influences animal health and welfare in the peripartal period (Farmer et al., 2017; Kemper, 2020; Björkman et al., 2022). The predominant clinical sign of PPDS is reduced milk production with or without mastitis and wasting piglets, which leads to an increased piglet mortality rate and therefore reduced number of weaned piglets (Koketsu et al., 2017; Niemi et al., 2017; Farmer et al., 2017; Kemper, 2020). Hence, this multifactorial disease complex has a major impact on the economic output of a sow herd (Papadopoulos et al., 2010; Jenny et al., 2015; Niemi et al., 2017; Farmer et al., 2017; Grahofer et al., 2020; Kemper, 2020; Björkman et al., 2022). A lack of crude fiber in the diet, reduced water consumption, prolonged farrowing, and urogenital tract infection are some of the main risk factors leading to PPDS in sows (Papadopoulos et al., 2010; Farmer et al., 2017; Grahofer et al., 2020, 2021; Kemper, 2020; Björkman et al., 2022). The incidence of PPDS within a herd varies from only few sporadic cases to epidemic outbreaks up to 60% (Pendl et al., 2017; Kemper, 2020). The diagnosis of PPDS should not only be based on an increased body temperature above 39.5 within 12 to 48 h postpartum, but also should include the general behavior of the sows and offspring as well as alteration of the mammary gland (reddening, swelling,..) (Pendl et al., 2017; Farmer et al., 2017; Kaiser et al., 2020; Kemper, 2020; Spiegel et al., 2022b). The main treatment includes a combination of nonsteroidal anti-inflammatory drugs and pharmacological oxytocin to reduce the pain in sows and to maintain milk production and suckling behavior (Pendl et al., 2017; Kemper, 2020). Prophylactic use of nonsteroidal anti-inflammatory drugs has been shown to numerically reduce the risk of PPDS by greater than 10% (Plush et al., 2018). Only if this treatment regime is not successful or the general health status of the sow reduces, antibiotics should be administered (Pendl et al., 2017). To reduce the treatment incidence, prophylactic measures should be implemented after defining the farm specific risk factors (Jenny et al., 2015; Pendl et al., 2017; Farmer et al., 2017; Kemper, 2020; Björkman et al., 2022). Recent studies have been conducted to estimate the risk for PPDS in sows before and after farrowing but currently, no reasonable and suitable predictor variables are available for the swine industry (Spiegel, 2016; Kaiser et al., 2018, 2020; Björkman et al., 2022; Spiegel et al., 2022b).

Diagnostic measures for the mammary gland

Routine clinical evaluation of the mammary gland is based on inspection and palpation of the udder (Kaiser et al., 2020; Spiegel et al., 2022b). For further diagnostics, macroscopic and bacteriological investigation of milk secretion can be conducted (Spiegel et al., 2022a). However, their diagnostic use is minimal, because milk samples from healthy sows contain the same microbiota as those from mastitis-infected sows (Kemper and Gerjets, 2009). Therefore, a recent study evaluated if mammary gland biopsy would be a better approach as it would reduce sample contamination (Spiegel et al., 2022a). No differences in the contamination of pathogens between the milk sample and the biopsy could be detected. Recently, several new diagnostic tools have been tested to objectively describe disorders of the mammary gland in sows (Spiegel et al., 2022a) with numerous studies evaluating both infrared thermography and ultrasonography for an adequate diagnostic assessment (Sporn, 2013; Spiegel, 2016; Peltoniemi et al., 2020; Latynina et al., 2021; Rosengart et al., 2022; Spiegel et al., 2022b). Data from infrared thermography studies have yielded controversial results. This technique detects diseased sows and disorders in the mammary gland, however, skin lesions of the udder can lead to misinterpretation (Latynina et al., 2021; Rosengart et al., 2022; Spiegel et al., 2022b). Ultrasonographic examination can be used for a detailed description of the mammary gland (Figure 3) and clinical diagnosis of alterations, such as mammary gland oedema, monitoring teat health, or chronic lesions (Sporn, 2013; Peltoniemi et al., 2020; Spiegel et al., 2022b). Measurement of the mammary gland parenchyma by ultrasonographic examination correlates positively with the measurement of the mammary gland by tape (Farmer et al., 2017). Furthermore, the weight of the parenchymal tissue of the mammary gland can be estimated (Farmer et al., 2017). The procedure is however very time consuming and lacks in the sensitivity for diagnosing acute mastitis in sows (Spiegel, 2016). Currently, there are no ultrasonographic parameters available that can predict or measure the milk yield of sows (Sporn, 2013). Hence, further research is needed to obtain parameters that can be used to objectively describe the health status of the mammary gland and estimate milk yield.

Conclusions

The developing gilt needs to be managed in a way that supports optimal mammogenesis to maximize lifetime milk production. There is a vast interplay of endocrine factors that are responsible for initiating and maintaining lactation. Sows display a higher nursing frequency with a shorter milk ejection phase than observed in other species which means there are many species-specific behaviors observed during lactation in the pig. The piglet is also responsible for the establishment and maintenance of milk production at the individual gland level. This means that care should be given to ensure each piglet is a strong nurser to stimulate maximal milk production. Lactation failure is an issue of increasing importance within the international swine industry and is largely caused by PPDS. Risk factors and diagnostic tools are being investigated but further work is required.

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