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The Protein Component of Sow Colostrum and Milk

P.K. Theil and W.L. Hurley

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Abstract

The production of colostrum and milk by the sow are primary limiting factors affecting survival, growth and development of the piglets. The proteins of colostrum and milk provide not only a supply of amino acids to the neonate but also a wide range of bioactive factors. Proteins in sow mammary secretions include those associated with the milk fat membranes, caseins, mammary-derived whey proteins, immunoglobulins, hormones and growth factors, enzymes, and a wide range of other proteins. Concentrations of most milk-specific proteins typically are lower in colostrum than in milk, while concentrations of immunoglobulins and other bioactive proteins often are enriched in colostrum compared with mature milk. Dietary protein is utilized for milk protein production with approximately 50% efficiency. During both the colostrum period and at peak lactation as much as 700–800 g of protein is secreted daily by today's highly prolific sows. Estimates of daily milk protein secretion during lactation suggest that sows are not able to consume sufficient dietary protein and energy to account for output of solids in milk and therefore must mobilize body protein and body fat to support their milk production. Milk protein content typically is not affected by dietary treatment, indicating that the sow mobilizes her body reserves to maintain milk production and milk protein production. These observations are of particular interest for today's highly prolific sows, which may require more dietary protein than previous genotypes.

Keywords: Colostrum, milk, protein, sow, lactation

1. Introduction

The newborn piglet is completely reliant on the sow's colostrum and milk for a nutrient supply as well as for a range of bioactive factors that impact its immunological and physiological development. Production of colostrum and milk by the sow are primary limiting factors

affecting survival, growth and development of the piglets [1–6]. Milk production by sows is impacted by numerous factors, including litter size, piglet size, nursing frequency, stage of lactation, sow age, body condition and parity, maternal behavior, and nutrition [7–10].

General composition of sow colostrum and milk has been reviewed previously [11–16]. Composition of mammary secretions after giving birth changes rapidly. For the sow, colostrum is considered as the secretions during the first 24 h after giving birth [17]. The period between 24 and 96 h after parturition is considered as transition milk [18, 19].

Recently, the lactation curve of sows was described [20], which showed that milk yield increases day by day in the first two weeks of lactation, depending on the number of suckling piglets. Indeed, genetic selection for large litters has increased the milk yield of sows and at peak lactation highly prolific sows (14 suckling piglets) produce on average 13–15 kg of milk daily. The milk protein production increases in a pattern similar to the lactation curve and peaks at 700–800 g of protein secreted daily.

The proteins of colostrum and milk provide not only a supply of amino acids to the neonate but also a wide range of bioactive factors. This chapter provides an overview of the proteins found in sow colostrum and milk, and a description on how the milk protein changes over time during the colostrum and lactation periods. In addition, estimates of milk protein production by the sow are discussed, and some of the factors that may impact milk protein production.

2. Proteins in milk fractions

The proteins of milk generally are characterized according to how they segregate during some fundamental methods of fractionating milk components. These methods originally were developed to fractionate bovine milk. One basic method of separating the fractions of milk is to separate the lower density lipid-containing cream fraction from the aqueous component, typically by centrifugation. The residual aqueous or defatted fraction then is referred to as the skim milk fraction. This type of fractionation has most often been used as a starting point for identifying milk proteins.

Milk is a partially stable emulsion of fat globules. In addition to the lipid component of the fat globules (primarily triacylglycerides), they also contain numerous proteins, which are associated with the milk fat globule membrane (MFGM). The MFGM proteins have been extensively studied in cow milk [21–23]; however, they have received relatively less attention in sow milk. Seventeen proteins have been identified in association with sow MFGM, including xanthine dehydrogenase, lactadherin, butyrophilin, adipophilin, acyl-CoA synthetase, fatty acid-binding protein 3, and others [24].

The skim milk fraction will contain the major milk protein components, including the caseins and whey proteins. Caseins are a special set of proteins found only in milk and are the major proteins found in sow milk. The caseins in sow milk include α S1-casein (CSN1S1), α S2-casein (CSN1S2), β -casein (CSN2), and κ -casein (CSN3). The whey proteins

are defined as all of the skim milk proteins excluding the caseins. The whey protein fraction encompasses a wide range of proteins with an extensive array of functions. The functionality of the various whey proteins includes direct involvement in the process of milk synthesis, provision of immune protection to the neonate, and hormones and growth factors that may impact neonatal development as well as enzymes and other proteins associated with cellular functions arising from epithelia, leukocytes, and other mammary tissue cells.

3. Major sow milk proteins

The concentration of total casein as a proportion of total milk protein generally increases from a low of 9–32% at parturition to 30–45% at 24 h postpartum [25, 26] and accounts for 50–55% of total milk protein in mature milk [25–28]. Total whey protein content of sow colostrum may be as high as 90% at parturition, followed by a decline to 70% by 24 postpartum [18, 26]. Total whey protein as a percentage of total protein is approximately 50% in mature milk [26].

The major whey proteins in sow milk include β -lactoglobulin (*BLG*), α -lactalbumin (*LALBA*), whey acidic protein (*WAP*), lactoferrin (also referred to as lactotransferrin; *LTF*), serum albumin (*ALB*), and immunoglobulins. *BLG* is a member of the lipocalin family, which transports small hydrophobic molecules; however, the specific function of this protein in milk or in the neonate is not understood. *BLG* has significant sequence similarity with glycodelin [29], also known as progesterin-associated endometrial protein (*PAEP*). Isolated bovine *BLG* has also been shown to have antimicrobial activity against some mastitis causing bacteria [30]. Concentrations of *BLG*, the major whey protein in sow milk, are between approximately 8 and 15 g/L during the initial week postpartum [31, 32]. *LALBA* is a small molecular weight protein that is the regulatory subunit of the lactose synthase enzyme activity. *LALBA* binds with β -1,4-galactosyltransferase in the Golgi apparatus of the mammary epithelial cell resulting in the synthesis of the disaccharide lactose from glucose and galactose. The synthesis of lactose, the primary osmole in sow milk, is responsible for drawing water into the Golgi apparatus and secretory vesicles during milk synthesis. Concentrations of *LALBA* are lower in colostrum (0.8–1.9 g/L) than in transition or mature milk (approximately 2–3 g/L) [31, 32], consistent with the observed lower concentrations of lactose in colostrum compared with mature sow milk. The function of the *WAP* in sow milk also is not understood. Concentrations of *WAP* in sow mammary secretions increase from 0.3 g/L at parturition to approximately 1 g/L at day 7 [31, 32]. Lactoferrin is an iron-binding protein with antimicrobial properties. Concentrations of lactoferrin in colostrum are relatively high (1.2 g/L) until day 3 postpartum and then decline to 0.3 g/L by one week postpartum [33]. Colostrum concentrations of albumin decline rapidly between parturition and 12 h postpartum (from 19 down to 8 g/L) and then gradually decline to 3.0 g/L or less [34].

4. Protective and bioactive proteins

Colostrum and milk contain an array of protective factors that can impact the neonate. The role of colostrum and milk immunoglobulins in the neonate has been extensively studied. The immunoglobulins are transported through the mammary epithelial cells by a receptor-mediated process, thought to involve the neonatal Fc-receptor (FcRn) in the case of IgG1 and IgG2, and the polymeric immunoglobulin receptor (pIgR) for IgA and IgM (see Ref. [35] for review).

Colostrum during or immediately after parturition contains the highest concentrations of each immunoglobulin, with average concentrations of total IgG, IgA, and IgM of approximately 65, 13, and 8 g/L, respectively [16]. These immunoglobulin concentrations remain elevated during the initial 6 h postpartum, decline by approximately 30–45% by 12 h, and continue declining through the next several days. Concentrations of IgG and IgM in mature milk are approximately 1 and 1.6 g/L, respectively. Interestingly, IgA is the major immunoglobulin in mature milk of the sow with a concentration of approximately 4 g/L [16]. The changes in proportion and total amount of immunoglobulins in sow mammary secretions are shown in **Figure 1**.

Figure 1. Relative total amounts and proportions of immunoglobulins G, A, and M in sow mammary secretions during lactation. Circles for 6 h through ≥12 days represent the total immunoglobulin content in mammary secretions compared with the content at 0 h. Adapted from Ref. [16].

Milk contains a wide array of antimicrobial and immunomodulatory proteins and peptides. Certainly the immunoglobulins, especially IgA, lactoferrin and lysozyme activity individually and synergistically probably provide for some of the antimicrobial function that has been found in sow milk [36]. Lysozyme activity has been identified in sow colostrum immediately after parturition [37] but not in mature milk [38]. Even some of the proteins associated with the milk fat globule may have bactericidal properties, such as the mucins [39, 40], lactadherin, butyrophilin, adipophilin, acyl-CoA synthetase, and fatty acid-binding protein 3 [24]. The specific role of these proteins in modulating the immune health of the sow's mammary gland and the health of her litter deserve additional evaluation. Several cytokines have been identified in sow colostrum and milk, including IL-4, IL-6, IL-10, IL-12, IFN- γ , TNF- α , and TGF- β [41]. Concentrations of these cytokines are greatest in colostrum and then decline as lactation progresses [41]. Butyrophilin has also been implicated as having an immunomodulatory function [42].

Milk contains many hormones and growth factors, which may have biological activity in the neonate [43, 44]. Prolactin in sow colostrum is at its highest concentration just prior to parturition and then declines rapidly during the first 24 h postpartum [45], followed by a slower decline through the remainder of lactation [46]. Similarly, concentrations of relaxin are greatest in colostrum and then decline over the first week of lactation [47]. This milk-borne relaxin has been associated with maternal programming of neonatal development in what is called the lactocrine hypothesis [48]. Specifically, relaxin absorbed into the circulatory system in the piglet prior to gut closure can affect the developing reproductive tract of the neonate. Leptin concentrations in the skim fraction of colostrum and milk decrease during the initial week of lactation before stabilizing for the remainder of lactation, while stage of lactation does not seem to impact leptin concentrations in whole milk [49]. Sow colostrum and milk also contain insulin, neurotensin, bombesin [50], triiodothyronine and thyroxine [51], insulin-like growth factor-I (IGF-I; [52]), epidermal growth factor-like peptide [53, 54], and prostaglandin-like activity [55].

Proteins in sow colostrum and milk include many enzyme activities, such as lipase and ribonuclease activity [38], trypsin inhibitor activity [56], ceruloplasmin [57], and enolase and glycogen phosphorylase [58]. A high molecular weight glycoprotein of unknown origin and function has been identified, which may be specific to sow milk [59].

5. Protein concentrations in sow mammary secretions

Sow colostrum, i.e. the mammary secretions during the first 24 h after onset of parturition, is rich in protein, especially colostrum from the earliest phase. The protein concentration drops from approximately 16 to 10% during the first 12 h after onset of parturition (**Figure 2**; [60]). Recent studies indicate that the protein content continues to decrease to reach a plateau at 6–7% protein at 36 h after parturition [61]. However, according to Ref. [60], the protein content remains rather stable in transient milk, i.e. in mammary secretions released from 24 h post parturition and the next couple of days (**Figure 2**). The low protein content of mammary secretions 24–36 h post parturition observed in Ref. [61] may indicate that late colostrum/

transient milk produced by modern hyperprolific sows, with an average of 18 piglets born, may be compromised in terms of protein content. In Ref. [60], published in 1995, sows had an average of 9.7 piglets born.

Figure 2. Examples of mammary secretion protein concentration change during the initial 12 h of the colostrum period and during the transition milk period. (A) Changes in colostrum protein concentration from parturition to 12 h can be described by $y = 0.0757x^3 - 1.3411x^2 - 0.1717x + 163.25$ ($R^2 = 0.99931$). (B) Changes in protein concentration from 24 to 72 h can be described by $y = -0.0151x^2 + 1.5054x + 66.15$ ($R^2 = 1$). Adapted from Ref. [60].

Changes in the protein concentration of sow milk during lactation can be estimated using the mathematical model described in Ref. [20]. Milk protein concentrations decline from 7% at day 2 to reach a plateau at approximately 5%, which is then maintained through at least four weeks after parturition (Figure 3; [20]).

Figure 3. Milk protein concentration during lactation. The profile was calculated using the mathematical model developed in Ref. [20] with the following input: Dietary protein (16%).

As lactation progresses, other milk constituents than the protein fraction also change. Indeed, the milk lactose concentration increases slightly from 5.2 to 5.5%, while the milk fat concentration decreases from 8.0 to 6.3% from day 2 to 28, respectively [20]. As a consequence, the energy content of milk decreases in a curvilinear manner throughout lactation (**Figure 4**).

Figure 4. Milk energy content during lactation. The profile was calculated using the mathematical model developed in Ref. [20] with the following input: Dietary protein (16%).

The protein-to-energy ratio of the milk declines during the first week of lactation; however, there is a gradual increase thereafter until weaning (**Figure 5**). The protein-to-energy ratio may be indicative of the nutritive quality of sow milk to support piglet growth [19]. However, the relative consistency of the protein-to-energy ratio of sow milk through lactation may indicate that milk intake of individual piglets is the major determinant of piglet growth rather than milk composition per se.

Figure 5. Protein-to-energy ratio of sow milk during lactation. The profile was calculated using the mathematical model developed in Ref. [20] with the following input: Dietary protein (16%).

6. Daily protein yields in sow colostrum and milk

Recently, it was demonstrated that the yield of sow colostrum was approximately 50% higher than previously believed [4, 5, 17]. With the high protein content in colostrum secreted in the early phase (described above), the daily protein secretion through colostrum amounts to 700–800 g [61], which is similar to the daily secretion of protein in milk at peak lactation (see below; [20]). While recent studies have shed light on the amounts of nutrients being secreted through colostrum and when they are secreted [4, 61], it is still unknown when the colostral proteins are being synthesized [5]. The high concentration of protein in colostrum at parturition suggests that this synthesis occurs in late gestation, allowing for accumulation of the proteins in colostrum. Milk-specific proteins, such as the caseins, *BLG*, *LALBA*, and *WAP*, are synthesized by mammary epithelial cells, while most of the immunoglobulin and the serum albumin are synthesized elsewhere in the sow.

Figure 6. Daily milk yield of sows with litter size (LS) of 10, 12, or 14 piglets. Note that the profile was calculated using the mathematical model developed in Ref. [20], assuming that sows with 10, 12, and 14 piglets on average produced litter gain (LG) of 2.5, 2.8, and 3.1 kg/d, respectively.

From a nutritional perspective, the timing of synthesis of the colostral proteins is important because fetal growth, mammary growth, and colostrum protein production compete for the dietary proteins supplied during late gestation. Factorial calculations of the daily protein requirement in late gestation suggest that dietary protein likely is scarcely supplied [62]. In a recent study, colostrum yield and colostrum protein content were studied across five different experiments to reveal potential limitations in colostrum synthesis [63]. In that study, it was found that the colostrum yield was positively correlated with litter size (including total born, live born, and 24 h litter size), and it is therefore logical to suggest that highly prolific sows

may require more dietary protein than previous genotypes. However, no relationship between colostrum yield and colostrum protein concentration was found, indicating that colostrum protein production likely is not compromised, in spite of high colostrum production due to their large litters [63].

Daily milk production increases during the first two weeks of lactation and peaks around day 17 of lactation [20], although it seems to peak a few days later if the production level is lower. Milk yield is greatly affected by the number of suckling piglets [64] because each piglet takes ownership of a single mammary gland and stimulates mammary growth [65, 66] and maintains milk production within that gland [67]. Milk yield is around 13-15 kg/d at peak lactation in modern highly prolific sows (with 14 piglets; [20]), whereas sows with a more moderate litter of 10 suckling piglets and consequently less litter gain per day produce around 10 kg/d (**Figure 6**). Consequently, sows produce around or slightly above 1.0 kg of milk daily for each piglet at peak lactation. After peak lactation, the milk yield decreases; however, it remains nearly maximal if piglets are weaned after three to four weeks.

Figure 7. Daily milk protein yields of sows with litter size (LS) of 10, 12, or 14 piglets. Note that the profile was calculated using the mathematical model developed in Ref. [20], assuming that sows with 10, 12, and 14 piglets on average produced litter gain (LG) of 2.5, 2.8, and 3.1 kg/d, respectively.

Daily milk protein production increases in a fashion similar to the lactation curves of sows (**Figure 7**). Thus, the daily milk protein yield also peaks around day 17 (slightly later for sows with a lower yield). For highly prolific sows, as much as 750 g of milk protein is secreted daily, whereas the daily milk protein yield is around 500 g when sows have 10 suckling piglets and have a moderate level of productivity (i.e. litter gain of 2.5 kg/d). In a recent study, it was found that milk protein concentration was negatively related to the milk yield of highly prolific sows for all four weeks of lactation [63]. The negative relationship suggests that the mammary capacity for milk protein synthesis has been reached or, alternatively, that the dietary protein

supply is inadequate to support the milk production of high prolific sows. In favor of the latter explanation, it was demonstrated that dietary protein is utilized for milk protein production with approximately 50% efficiency [68]. At peak lactation, sows ingest around 1300–1400 g of dietary protein daily, but if high producing sows secrete 750 g of milk protein daily, they should ingest 1500 g/d of dietary protein (assuming 50% utilization efficiency). Most sows are not able to ingest enough feed to obtain a zero balance of protein nor a zero balance of energy, and consequently, sows typically mobilize body protein and body fat to support their milk production [19, 62, 68].

Milk production and milk protein production are highly prioritized by lactating sows [19]. If the dietary supply of protein or energy is insufficient, the sow mobilizes amino acids from muscle tissues or fat from adipose tissues, respectively. Mobilization of muscle tissues can be substantial and result in sow weight loss that in extreme cases may amount to 75–80 kg during three weeks of lactation [69]. However, in a pioneer experiment [70] where lactating sows were provided an insufficient nutrient supply, a linear decrease in weight loss was reported in sows in response to feed intake that was gradually increased from 1.5 to 4.8 kg/d (over six different feeding levels). In each case, the nitrogen balance of the sows was negative but was clearly responsive to feed intake. Interestingly, the milk protein content was not affected by dietary treatment, and the piglet growth rate, which may be seen as an indicator for the milk yield, was not compromised until the fourth week of lactation. These findings are consistent with the sow's physiology during lactation being set to maintain milk production and milk protein production as a high priority, and she compensates for insufficient nutrient intake by increasing the body mobilization. The reduced piglet weight gain in the fourth week of lactation observed in Ref. [70] could be interpreted as a result of the depletion of readily available body pools of amino acids after three weeks of insufficient nutrient supply.

7. Conclusion

Colostrum is much richer in protein than in mature sow milk. The protein component changes dramatically during the colostrum period, where the decline in contents of bioactive proteins, including immunoglobulins, hormones, and growth factors, is pronounced. The concentrations of milk-specific proteins, such as the caseins and the major mammary-derived whey proteins, increase during the early lactation period. The amount of protein secreted in colostrum and milk is extremely high. During both the colostrum period and at peak lactation as much as 700–800 g of protein is secreted daily. Currently, it is not known which factors are most limiting the sow milk production or the sow milk protein production. Without doubt, daily feed intake and dietary content of essential amino acids are important factors. However, sow live weight, body pools of amino acids in muscle tissues, and amino acid mobilization capacity may be equally important to sustain this demanding daily production of milk and milk protein. Current research suggests that today's highly prolific sows may require more dietary protein than previous genotypes.

Author details

P.K. Theil^{1*} and W.L. Hurley²

*Address all correspondence to: Peter.Theil@anis.au.dk

1 Aarhus University, Tjele, Denmark

2 University of Illinois, Urbana-Champaign, USA

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