9. Composition of sow colostrum and milk

W.L. Hurley University of Illinois, Agricultural Education Program, 430 Animal Sciences Laboratory, 1207 W. Gregory, Urbana-Champaign, IL 61801, USA; wlhurley@illinois.edu

Abstract

Components of milk include proteins, lipids, carbohydrates, minerals, vitamins, and cells. The contents of these components are affected by a variety of factors, with stage of lactation having the most dramatic influence on composition. Mammary secretions from the sow during the initial 24 h after parturition are generally higher in concentrations of immunoglobulins, some microminerals and vitamins, and hormones and growth factors, and lower in concentrations of lactose, when compared with mature milk. Fat concentration in sow milk is transiently increased during the period from day 2 to day 4 of lactation. The composition of milk after day 7 to day 10 is relatively stable for the remainder of lactation. Diet can affect some milk components, including concentrations of fat, fat-soluble vitamins and some minerals, as well as proportions of specific fatty acids. Genetics, parity, colostrum and milk yield, and ambient temperature have also been found to affect component composition of colostrum and milk. This chapter summarizes some of the literature available on sow colostrum and milk composition. Benchmark averages of component concentrations based on values reported in the literature are also provided.

Keywords: mammary gland, protein, fat, lactose, immunoglobulins

9.1 Introduction

In its fetal stage of development, the piglet relies on the sow as the source of all nutrients, growth stimulating factors and protective factors. Once it is born, the piglet continues to rely on the sow for many of those inputs through the secreted fluids from the mammary gland. Lactation function by the sow is a continuation of the maternal contribution to the growth and development of the piglet beyond the fetal stage. The critical importance of colostrum and milk for the newborn piglet has been well documented (Le Dividich *et al.*, 2005; Quesnel *et al.*, 2012; Theil *et al.*, 2014; see also Chapter 8; Quesnel *et al.*, 2015). The rapid development of the neonate coincides with the rapid changes in composition of mammary secretions consumed by the suckling piglet.

Components of milk include carbohydrates, lipids, proteins, minerals, vitamins, and cells. Such a superficial listing of milk components does not do justice to this exceptionally complex fluid. Milk is a medium through which the sow delivers to the neonate a readily consumed and easily digested source of energy in several forms, lipids, amino acids, minerals, vitamins and a range of biologically active components. This fluid is all the more remarkable when considered that it evolved to be rapidly synthesized, secreted,

ingested and digested. Milk is rapidly removed from the gland during the few seconds in which milk ejection occurs (Brooks and Burke, 1998), and quickly forms a curd once it enters the piglet's stomach. The milk components in the stomach must be passed into the intestine and mostly digested within 45 min in preparation for milk from the next suckling. The initial substrates that went through the complex cellular processes of synthesis of lactose, fat, protein, and other milk components to a great extent are digested and absorbed into the piglet's blood in less than a couple of hours after being synthesized.

This chapter focuses on composition of colostrum and milk of the sow, specifically the content of the many components found in these mammary secretions. Estimates of the concentration of components in colostrum and milk are affected by a number of factors. The factors that relate to how samples of mammary secretions are collected and analyzed are summarized in the section on Methodology. Physiological state of the mammary gland is a major determinant in the composition of mammary secretions, most clearly seen in the differences between colostrum vs. milk composition. Sections on each of the major components of mammary secretions are organized to address how composition changes with stage of lactation, as well as how other factors affect composition. For additional summary reviews of sow colostrum and milk composition, the reader is referred to Neuhaus (1961), Bowland (1966), Hartmann and Holmes (1989), and Darragh and Moughan (1998). Comparisons of sow milk composition with that of other species can be found in reviews by Oftedal (1984), Oftedal and Iverson (1995), and Park (2011).

The tables in this chapter provide the reader with average concentrations of components found in sow colostrum and milk, an indication of the range of reported values for the components, and a listing of sources used to derive the average concentrations. The tables are meant to provide representative values of the component concentrations based upon a collection of studies that, in most cases, have provided estimates of components at multiple points in lactation, or provided data that specifically focused on colostrum composition. The tables are not meant to be an exhaustive compilation of all studies that have evaluated composition. Table 9.1 includes the references from which reported values were used in calculating the average component content for colostrum in Table 9.2 (parturition to 24 h postpartum) and for milk in Table 9.3 (48 h postpartum and beyond).

9.2 Methodology

9.2.1 Sampling of mammary secretions

All studies that report colostrum or milk composition rely on some method of collection of the secretion. Collection of mammary secretions during parturition can be accomplished without administration of oxytocin to stimulate milk ejection. Endogenous oxytocin concentrations are elevated in a pulsatile manner during parturition (Gilbert *et al.*, 1994). Oxytocin administration becomes necessary to collect milk samples by about 6 h after birth of the first piglet (Jackson *et al.*, 1995). Administration of 10 to 80 IU oxytocin has been used, with the quantity depending on route of administration, such as intravenous (10 to 20 IU: Devillers *et al.*, 2004b; Theil *et al.*, 2004), intramuscular (20 to 40 IU; Jackson

Table 9.1. References used in calculating estimates of major component content for sow colostrum and milk for Table 9.2 and 9.3. The table represents an incomplete list of references reporting composition results for multiple days during lactation.

Reference	First sample vs. farrowing	Other samplings reported	Major components reported ¹
Perrin, 1955	at parturition	3, 6, 9, 12, 15, 18, 21, 24, 27, 30, 33-48 h; 3, 4, 5 d; 2, 3, 4, 5, 6, 7, 8 w	ts, lac, fat, pro, ash, snf
Elliott et al., 1971	w/in 12 h post-parturition	7, 14, 21 d	ts, lac, fat, pro, ash, snf
Mahan et al., 1971	13 d	21, 29 d	ts, lac, fat, pro, ash, snf
Fahmy, 1972	3 h post-parturition	14, 28, 25 d	ts, fat, pro, ash, ge
Coffey et al., 1982	24 h	72 h	fat
Boyd et al., 1982	birth 1st piglet	9, 18 d	ts, fat, pro
White et al., 1984	15 d	22 d	ts, lac, fat, pro, ge
Loudenslager et al., 1986	during parturition	2, 21 d	fat
Klobasa et al., 1987	prior to piglets suckling	6, 12, 18, 24, 48, 72 h; 5, 7, 14, 21, 28, 35, 42 d	ts, lac, fat, pro
Zou et al., 1992	w/in 8 h of birth 1st piglet	24 h; 7, 21 d	lac, fat, pro
Taugbøl et al., 1993	at parturition	14 d	fat
Jackson et al., 1995	birth 1st piglet	1, 2, 3, 4, 6, 9, 12, 18, 24, 48, 72, 169 h	lac, fat, pro
Csapo <i>et al.,</i> 1996	immediately post-parturition	12, 24, 48 h; 3, 5, 10, 20, 45-60 d	ts, fat, pro
Dourmad et al., 1998	3 d	7, 15, 22 d	ts, lac, fat, pro, ash, ge
Tilton et al., 1999	18 d		ts, fat, pro, ash, ge
Alston-Mills et al., 2000	3 d	21 d	lac, fat, pro
Kim and Mahan, 2001	at parturition	2, 3, 4, 5, 6, 7, 10, 14 d	pro
Noble et al., 2002	w/in 3 h end of parturition	6, 12, 24, 48 h; 3, 6, 9, 12, 21 d	ts, lac, pro
Devillers et al., 2004b	birth 1st piglet	6, 12, 24 h	ts, lac, fat, pro, ash, ge
Laws et al., 2009	w/in 4 h birth 1st piglet	3, 7, 14, 21 d	lac, fat, pro, ge
Farmer et al., 2010	3 d	20 d	ts, lac, fat, pro
Foisnet et al., 2010a	birth 1st piglet	3, 6, 24 h	ts, lac, fat, pro, ash, ge
Foisnet et al., 2010b	birth 1st piglet	6, 12, 24, 36, 48 h	ts, lac, fat, pro, ash, ge
Leonard et al., 2010	1 h after birth 1 st piglet	12 d	ts, fat, pro
De Quelen et al., 2010	w/in 12 h start of parturition	3, 7, 21, 32 d	fat
Ariza-Nieto et al., 2011	colostrum, not specified	7, 14d	fat, pro, ge
Foisnet et al., 2011	after birth 1 st piglet	6, 12, 24, 36 h	ts, lac, fat, pro, ash, ge
Krogh <i>et al.,</i> 2012	at parturition		ts, lac, fat, pro
Flummer and Theil, 2012	w/in 3 h birth 1 st piglet		ts, lac, fat, pro, ge
De Quelen et al., 2013	w/in 12 h start of parturition	7, 14, 21, 28 d	fat
Loisel et al., 2013	after birth 1 st piglet	24 h; 7, 21 d	ts, lac, fat, pro, ash, ge

 $^{^{1}}$ ts = total solids or dry matter; lac = lactose; fat = milk fat; pro = crude or total protein; ash = ash; ge = gross energy; snf = solids-not-fat.

et al., 1995; Klobasa et al., 1987), or intramammary injection (80 IU; Noble et al., 2002). Often piglets are removed from the sow for a time to allow for milk accumulation prior to milk collection (Klobasa et al., 1987). Others have used a milking machine to collect milk samples (Garst et al., 1999). In the latter case, time of day when sows are milked affects milk fat, protein and somatic cell concentrations (Garst et al., 1999). For a more detailed

description of ways to measure sow colostrum and milk yield, please refer to Chapter 8 on colostrum and milk production (Quesnel *et al.*, 2015). Milk typically is collected from a subset of functional glands or from all functional glands and a composite sample used for analysis. Concentrations of milk fat, protein and lactose do not vary significantly between front and rear mammary glands on the sow (Reynolds and Rook, 1977).

Milk composition can be affected by oxytocin administration, where intravenous administration of 20 IU oxytocin results in lower concentrations of total solids (dry matter), fat, lactose and energy compared with manual stimulation or 10 IU of oxytocin intravenous injection (Hartog *et al.*, 1987). Intravenous administration of oxytocin can result in lower milk fat concentrations compared with intramuscular oxytocin administration, but the route of administration does not affect milk protein concentration (Garst *et al.*, 1999). The composition of milk varies with the fraction that is removed during milk ejection, with the hind milk (portion removed in response to oxytocin injection after piglets completed suckling) having higher concentrations of total solids, fat, and energy, but not of protein and lactose, compared with the fore milk fraction (Atwood and Hartmann, 1992).

9.2.2 Analysis of major milk components

Many methods for determining the gross composition of milk are derived from the Official Methods of Analysis published by the Association of Official Analytical Chemists. A brief overview of methods used for milk component analysis is provided here. Total solids, or dry matter, is often determined gravimetrically after drying the milk sample, although freeze drying has also been used. Ash content is determined by incineration of the sample in a muffle oven at 550 °C. Fat percentage often has been determined using the Babcock method or Gerber method, both of which use sulfuric acid to hydrolyze organic components other than the lipid. The Babcock method has been noted as giving slightly lower fat values compared with a solvent extraction method (i.e. Mojonnier method; Fahmy, 1972). Other methods employ a solvent extraction approach such as using a Soxhlet apparatus or the Roese-Gottlieb or Mojonnier method which employs an extraction with ether or petroleum ether, followed by drying and weighing the extract. Methods for determining total milk protein have included the Kjeldahl method, or some modification of the Lowry protein assay (copper-binding assay), or modification of the Bradford protein assay (dye-binding assay), although more recent reports have used automated instruments that directly determine the N content. Lactose has been determined by reducing-sugar assays, by enzymatic hydrolysis, or by difference subtracting other components from the total solids value. Enzymatic analysis of lactose in milk samples is carried out by hydrolysis of lactose to D-glucose and D-galactose by β-galactosidase, followed by oxidation of D-galactose by nicotinamide-adenine dinucleotide and then measuring the absorbance of the reduced NADH. Total milk energy content typically is determined either directly by combustion using an adiabatic bomb calorimeter, or by calculation from percentages of milk fat, total protein, and lactose (Klaver et al., 1981). More recent reports have used methods that employ Fourier Transform Infared analysis (Krogh et al., 2012).

9.3 Physico-chemical properties

Specific gravity of sow colostrum at parturition starts at approximately 1.06 g/ml, reflecting the high concentration of total protein at that time. It then declines within the first day and stabilizes at about 1.035 g/ml throughout much of lactation, before rising slightly in an extended lactation beyond 6 weeks (Fahmy, 1972; Krakowski *et al.*, 2002; Sheffy *et al.*, 1952; Whittlestone, 1952). The pH of sow colostrum is more acidic than that of milk. Kent *et al.* (1998) reported that the pH of colostrum immediately before and after parturition was 5.7, rising to 6.0 at day 1, and reaching 6.9 by day 9, consistent with other reports (Coffey *et al.*, 1982; Miller *et al.*, 1971). Others have reported more basic ranges of pH for sow milk, even with pH above 7.0 (DeRouchey *et al.*, 2003; Sheffy *et al.*, 1952; Whittlestone, 1952). The pH of milk is related to the equilibrium of calcium between the aqueous and casein micellar phases (Gaucheron, 2005).

There are limited reports describing other physico-chemical properties of sow colostrum or milk. Viscosity of sow colostrum is highest at parturition and then declines, with estimates of milk viscosity at 3.855 millipascal-seconds (Whittlestone, 1952). Conductivity increases during the initial day of parturition, and then declines slowly to about day 16 of lactation, where the average conductivity of sow milk is estimated at 3.248 ohm⁻¹×10³ (Whittlestone, 1952). The freezing point of cow milk is often used as a means to determine if water has been added to the milk. For sow milk, the freezing point is estimated at -0.563 °C (Sheffy *et al.*, 1952).

9.4 Water and total solids

Water is a critical component of mammary secretions. It provides a medium for mixing of the other components during milk synthesis and secretion, as well as for providing this nutrient to the young. The secretion of water as part of milk is closely linked with the synthesis and secretion of the major milk carbohydrate in mammary secretions, namely lactose. Total solids or dry matter content of mammary secretions are typically reported rather than water content. Total solids or dry matter are determined gravimetrically by evaporating the water from the secretion sample, usually at temperatures below 100 °C. Therefore, estimates of total solids content include all organic and inorganic components of mammary secretions.

9.4.1 Stage of lactation

Accounting for the total solids content of mammary secretions of the sow (Table 9.2), water makes up approximately 73% of the secretion mass during and immediately after parturition. Water content then increases to about 80% by 12 h postpartum and remains in the 77 to 81% range throughout lactation (Table 9.3). The increase in water content during the initial day postpartum occurs as a result of the rapidly declining concentration of proteins, primarily immunoglobulins, which is only partially offset by the increase in lactose content during the same period (Table 9.2).

Table 9.2. Average and range of reported concentrations of major components of sow colostrum.

Colostrum	Time from part	curition (h)				
	01	3-4	6	12	18	24
Total solids %						
Average ²	26.7	28.1	23.8	20.1	18.4	20.1
Range ³	24.0-30.2	26.7-28.9	21.8-26.6	18.4-21.6	17.7-19.4	17.2-23.4
Studies ⁴	12	3	4	4	2	11
Total protein %						
Average	16.6	16.7	13.8	9.6	9.4	7.7
Range	13.8-19.7	12.7-19.1	11.3-16.5	5.6-13.2	7.2-13.6	3.3-10.5
Studies	14	4	6	5	3	13
Fat %						
Average	6.4	6.1	5.9	5.9	6.4	8.0
Range	4.9-10.9	5.5-7.3	4.8-7.8	4.9-7.2	5.2-7.0	5.6-11.6
Studies	16	4	4	6	3	11
Lactose %						
Average	2.8	2.7	3.0	3.6	4.1	3.9
Range	2.4-3.2	2.4-3.2	2.6-3.2	3.3-4.1	3.9-4.4	3.6-4.3
Studies	10	5	6	5	3	11
Ash %						
Average	0.68		0.63	0.64		0.67
Range	0.54-0.70		0.61-0.68	0.63-0.66		0.61-0.68
Studies	7		4 (3-6h)	4 (8-14h)		8
Energy kJ/g						
Average	6.7		6.0			5.7
Range	5.5-8.3		5.2-6.7			4.6-6.4
Studies	7		2 (4-6h)			8

¹ Defined as one of the following: immediately prior to parturition, at the birth of the first piglet, or during parturition.

Total solids content is highest during the initial 4 to 6 h after parturition and then declines to about 20% of the mass of the mammary secretions by 12 h (Table 9.2). The transient increase in total solids to 22 to 23% on days 2 and 3 reflects a peak of fat percentage that occurs at that time. Total solids then remain at approximately 19% through the remainder of lactation. Solids-not-fat (SNF) is determined as the difference between total solids percentage and fat percentage. The SNF content provides a crude estimate of the non-

² Average of values from studies that included mammary secretion sampling at the respective time relative to parturition.

³ Range of values from studies included in determining the average value.

⁴ Number of studies included in determining the average value. Values are from mean of multiple animals (such as from Perrin, 1955) or multiple experiments (such as from Jackson *et al.*, 1995), from control groups when the study included experimental treatments, or from overall component concentrations when given. References used to calculate average are listed in Table 9.1.

Table 9.3. Average and range of reported concentrations of major components of sow milk.

Milk	Day of lactation	on					
	21	3	7	12-15	20-22	27-29	42-60
Total solids %							
Average ²	22.1	22.7	19.3	20.0	19.5	18.8	19.5
Range ³	18.6-27.6	19.0-27.0	18.3-20.4	18.2-22.0	17.3-23.2	17.3-20.9	17.0-21.0
Studies ⁴	5	6	5	4	8	4	6
Total protein %							
Average	7.5	6.5	5.4	5.3	5.0	5.3	6.5
Range	5.4-10.4	4.6-9.9	3.6-6.4	4.7-7.1	3.6-6.0	5.36-5.4	5.4-8.2
Studies	7	10	9	12	9	3	6
Fat %							
Average	10.1	9.7	7.6	7.4	7.5	7.0	7.1
Range	6.5-12.9	5.4-13.0	4.5-8.8	5.3-10.8	5.0-11.5	5.2-9.8	5.3-8.8
Studies	5	9	11	10	16	6	6
Lactose %							
Average	4.3	4.6	5.2	5.2	5.1	5.6	5.0
Range	4.0-4.5	3.8-5.3	4.7-5.6	5.1-6.3	4.0-5.8	4.9-6.0	4.3-5.7
Studies	5	8	8	7	13	3	5
Ash %							
Average	0.75	0.79	0.81	0.90	0.86	0.89	1.02
Range	0.75-0.76	0.74-0.82	0.76-0.87	0.77-1.33	0.76-0.95	0.82-1.06	0.84-1.14
Studies	3	3	3	5	5	4	4
Energy kJ/g							
Average	6.5	6.0	5.4	4.9	5.0	4.4	
Range		5.5-6.5	5.1-5.6	4.6-5.3	4.2-5.1	4.2-4.7	
Studies	1	3	4	5	6	2	

¹ Defined as approximately 48 h post-parturition or >24 h after birth of the first piglet.

fat milk components, primarily representing protein, lactose and ash. Reporting of SNF content was prevalent in earlier studies (see Table 9.1 for sample references), however, more recent studies have either reported each major milk component separately or focused on measuring one or two specific components, such as fat or immunoglobulin content.

² Average of values from studies that included mammary secretion sampling at the respective time relative to parturition.

³ Range of values from studies included in determining the average value.

⁴ Number of studies included in determining the average value. Values are from mean of multiple animals (such as from Perrin, 1955) or multiple experiments (such as from Jackson *et al.*, 1995), from control groups when the study included experimental treatments, or from overall component concentrations when given. References used to calculate average are listed in Table 9.1.

9.4.2 Diet and other factors

Effects of diet and environmental factors on total solids content of sow milk have been reported. Some studies have observed that source of supplemental dietary energy can affect total solids content of milk (Van den Brand *et al.*, 2000; White *et al.*, 1984). Other studies have found no effect of feeding supplemental dietary energy during lactation in the form of cornstarch (Coffey *et al.*, 1982) or animal fat on milk total solids (Coffey *et al.*, 1982; Theil *et al.*, 2004). Feeding crude glycerol (up to 6.77%) to sows tended to increase milk total solids at day 18 of lactation (Schieck *et al.*, 2010). Dietary fiber level during gestation does not affect total solids content of colostrum or milk (Loisel *et al.*, 2013). Dietary salt level (0.1 vs. 0.4%) fed prepartum and during lactation affects water intake by sows, however, does not affect milk total solids at d 18 of lactation (Seynaeve *et al.*, 1996). Milk total solids content is affected by ambient temperature, with total solid percentage being lower at 20 vs. 29 °C (Renaudeau and Noblet, 2001).

9.5 Carbohydrates

Lactose is the major carbohydrate in sow milk. It is also the major osmole in milk. Its synthesis in the mammary epithelial cell is responsible for drawing water into the secretory vesicles (Peaker, 1983). Lactose also is considered as the least variable component of milk, with concentrations typically remaining within a narrow range. Milk lactose content has a lower coefficient of variation among sows than that of fat or protein (Atwood and Hartmann, 1992).

9.5.1 Stage of lactation

Lactose concentrations are low in colostrum during the initial few hours postpartum relative to mature milk (Table 9.2 and 9.3). Concentrations of lactose then increase gradually over the first two to three days of lactation. This period coincides with the later stages of lactogenesis (discussed below). This also is the period when activity of lactase, the major intestinal enzyme that hydrolyzes lactose in the neonate, is increasing (Chapter 15; Le Huërou-Luron and Ferret-Bernard, 2015). Lactose concentrations may decline in extended lactations of 7 to 8 weeks (Table 9.3), however, only limited information is available for that period.

Glucose concentration in sow mammary secretions is low (18 to 135 μ g/ml; Atwood and Hartmann, 1995) relative to lactose concentration (27 to 56 mg/ml; Table 9.2 and 9.3). Glucose concentration increases from a low at parturition to a peak at about day 3 of lactation, before declining again through day 5 (Atwood and Hartmann, 1995). Glucose-6-phosphate increases in concentration rapidly after parturition and remains elevated through day 5, while glucose-1-phosphate concentrations decline soon after parturition. Galactose concentration is highest in colostrum and decreases to day 5 of lactation (Atwood and Hartmann, 1995).

Sow milk also contains complex carbohydrates, including 29 distinct oligosaccharides (Tao *et al.*, 2010). Concentrations of these oligosaccharides are highest in colostrum, and then decline during lactation before increasing again by day 24. In addition, the profiles of oligosaccharides in sow milk vary with stage of lactation.

9.5.2 Diet

Gestation diet composition might be expected to affect colostrum and possibly milk lactose content. However, lactose concentration in colostrum or milk is not affected by gestation diets supplemented with energy in the form of oils (Jackson *et al.*, 1995; Laws *et al.*, 2009), nor is it affected by gestation diets supplemented with conjugated linoleic acid (Krogh *et al.*, 2012) or with the leucine metabolite β -hydroxy β -methyl butyrate (Flummer and Theil, 2012). Gestation diets with high dietary fiber content (23.4%) do not affect colostrum or milk lactose concentrations (Loisel *et al.*, 2013).

Feeding supplemental dietary fat during lactation has no effect on milk lactose content (Coffey et al., 1982; Lauridsen and Danielsen, 2004; Theil et al., 2004). Lactose concentration in sow milk is not affected by protein level, lysine level or branched chain amino acid levels in lactation diets (Dourmad et al., 1998; King et al., 1993; Richert et al., 1997). However, lactose content of sow milk is affected by energy source, with feeding starch resulting in a higher lactose percentage than feeding tallow (Van den Brand et al., 2000). Lactose concentration in milk at day 22 is higher in sows fed high fructose diets during lactation compared with control or high dextrose diets (White et al., 1984). Lactation diets supplemented with glycerol increase milk lactose content (Schieck et al., 2010).

Dietary folic acid supplementation has been observed to decrease milk lactose at day 7 of lactation (Wang *et al.*, 2011), however, it should be noted that lactose concentrations in that study were lower than typically reported by others (Table 9.3). Lactose concentration of milk at day 10 to 12 of lactation is not affected by dietary electrolyte balance (DeRouchey *et al.*, 2003).

9.5.3 Other factors

Zou *et al.* (1992) noted lower lactose concentrations in colostrum of first lactation Meishan sows compared with Yorkshire sows. Concentrations of lactose in milk were reported not to be different among those breeds (Alston-Mills *et al.*, 2000; Zou *et al.*, 1992), however, were found to be greater in milk from 50% Meishan crossbred sows compared with Yorkshire sows (Farmer *et al.*, 2001). Lactose concentration in sow colostrum is associated positively with colostrum yield (Foisnet *et al.*, 2010a). Similarly, lactose content of milk at day 22 of lactation is positively correlated with milk yield (r=0.33, *P*<0.1; White *et al.*, 1984). Lactose concentrations of sow milk are not affected by parity (Baas *et al.*, 1992; Goransson, 1990: Klobasa *et al.*, 1987), sow body condition (Klaver *et al.*, 1981), or ambient temperature (Renaudeau and Noblet, 2001).

9.6 Lipids

The fat content of mammary secretions is considered as the most variable of the components. This is particularly apparent in considering the effects of stage of lactation, diet and other factors on fat content of colostrum and milk.

9.6.1 Stage of lactation

Averaging the fat, or lipid concentrations of mammary secretions that have been reported in the various studies listed in Table 9.1 gives a profile of that component through lactation (Table 9.2 and 9.3). Among the studies summarized in Table 9.2, fat percentage of colostrum at parturition ranges from 4.9 to 10.9%, with an average of 6.4%. Average fat content remains at the 5.9 to 6.4% level until 18 h postpartum and then increases to about 8% by 24 h. A transient peak of fat content is seen in most studies, occurring typically between 24 h and day 3 postpartum, although some studies report continued elevated fat percentages even at day 7. Fat concentrations as high as 13% have been reported at day 3 (Csapo *et al.*, 1996). This elevation of fat in mammary secretions coincides with a phase of transient milk identified as occurring in the period between the colostrum phase (parturition to 24 h postpartum) and about day 4 of lactation (Theil *et al.*, 2014). Average fat percentage is relatively stable at 7.0 to 7.6% from day 7 through 6 to 8 weeks of lactation (Table 9.3), a period when mature milk is present (Theil *et al.*, 2014).

Average concentrations of the major fatty acids in sow milk are indicated in Table 9.4. Concentrations of fatty acids in sow colostrum have been reported by Csapo *et al.* (1996). When comparing fatty acid proportions in colostrum (at parturition) and day 20 of lactation, the increases in proportions of C16:0, C16:1 and C18:3 during lactation are partially offset by decreases in proportions of C18:1 and C18:2. Sow mammary secretions contain only trace amounts of short and medium chain fatty acids up to C12:0 (Csapo *et al.*, 1996; Hartog *et al.*, 1987; Lauridsen and Danielsen, 2004). Csapo *et al.* (1996) found that less than 0.25% of total fatty acids were composed of the short and medium chain fatty acids C4:0 through C12:0. Others have reported proportions of C10:0 and C12:0 of up to 0.36 and 0.49% of total fatty acids, respectively (Lauridsen and Danielsen, 2004).

9.6.2 Diet

The primary impact of diet on colostrum or milk composition occurs through an effect on milk fat content. Gestation diets might be expected to impact colostrum composition and perhaps have a carry-over effect into lactation. On the other hand, lactation diets might be expected to impact colostrum composition only if feeding of the diet was initiated prepartum. Lactation diets would be expected to impact sow milk composition. Some studies have found that supplemental dietary fat increases milk fat percentage in sow mammary secretions (Boyd *et al.*, 1982; Pettigrew, 1981; Shurson and Irvin, 1992; Shurson *et al.*, 1986), while other studies have not found a significant effect of feeding supplemental dietary fat during late gestation and lactation on the percentage of milk fat (De Quelen *et al.*, 2010, 2013; Farmer *et al.*, 2010; Jackson *et al.*, 1995; Lauridsen and Danielsen, 2004; Leonard *et al.*, 2010; Miller *et al.*, 1971; Schieck *et al.*, 2010; Seerley *et*

Table 9.4. Average and range of reported proportions of amino acids in sow colostrum and milk and fatty acids in sow milk.

	Amino acids (% of total	protein) ¹	Fatty acids (% of total fatty acids) ²		
	Colostrum (range)	Milk (range)		Milk (range)	
Alanine	4.6 (4.4-4.8)	3.4 (2.8-3.9)	C14:0	4.05 (2.3-6.4)	
Arginine	5.9 (5.6-6.1)	5.2 (4.6-5.8)	C16:0	29.3 (17.0-37.0)	
Aspartic acid	8.6 (7.9-9.3)	8.1 (7.3-8.6)	C16:1	9.8 (7.4-13.8)	
Cystine	1.8 (1.7-1.8)	1.5 (1.3-1.7)	C18:0	4.41 (2.6-6.0)	
Glutamic acid	17.8 (17.5-18.1)	22.0 (18.9-28.8)	C18:1 ³	32.07 (29.4-39.2)	
Glycine	3.6 (3.1-4.0)	3.2 (2.3-3.6)	C18:2n-6	15.69 (8.9-25.9)	
Histidine	2.5 (2.1-3.3)	2.9 (2.3-3.9)	C18:3n-3	1.38 (0.6-2.9)	
Isoleucine	3.4 (2.4-3.9)	4.0 (2.9-4.4)	C20:4n-6	0.50 (0.1-0.9)	
Leucine	9.7 (9.1-10.2)	8.8 (8.1-10.1)	C20:5n-3	0.38 (0.2-0.6)	
Lysine	6.7 (6.3-7.3)	7.3 (7.0-7.9)	C22:5n-3	0.39 (0.2-0.7)	
Methionine	1.5 (1.2-1.7)	1.8 (1.4-2.0)	C22:6n-3	0.86 (0.2-2.1)	
Phenylalanine	4.4 (4.1-4.6)	3.9 (3.6-4.2)			
Proline	9.9 (9.1-10.6)	11.9 (10.9-12.3)			
Serine	6.8 (6.5-7.0)	5.3 (4.5-5.8)			
Threonine	5.9 (5.2-6.8)	4.1 (3.6-4.4)			
Tryptophan	1.9 (1.6-2.2)	1.4 (1.3-1.6)			
Tyrosine	5.0 (4.0-6.1)	4.2 (3.9-4.9)			
Valine	5.8 (5.0-6.3)	4.9 (3.9-5.5)			

¹ For amino acids, colostrum was from within 12 h of parturition, milk is from day 17 to day 28. References used to calculate averages: Bowland, 1966; Csapo et al., 1996; Dourmad et al., 1998; Dunshea et al., 2005; Elliott et al., 1971; King, 1998.

al., 1981; Theil et al., 2004; Tilton et al., 1999). Supplementation of sow diets with long-chain triglycerides increases milk fat content compared with medium-chain triglycerides (Azain, 1993). Colostrum fat percentage can be increased by supplementing the late gestation diet with conjugated linoleic acid (Krogh et al., 2012). Milk fat is affected by dietary energy intake (Noblet and Etienne, 1986; Schoenherr et al., 1989), and by source of dietary energy (Coffey et al., 1987; Van den Brand et al., 2000). On the other hand, neither dietary crude protein intake nor dietary lysine level affect sow milk fat (Dourmad et al., 1998; Kusina et al., 1999). However, milk fat concentration is affected by dietary intake of branched chain amino acids (Richert et al., 1997) and, by day 14 of lactation, it is affected by dietary supplementation of folic acid (Wang et al., 2011). Feed restriction of sows during the two weeks prepartum significantly increases fat percentage in colostrum collected before 15 h postpartum (Goransson, 1990).

² For fatty acids, milk is from day 7 to day 20. References used to calculate averages: Csapo *et al.*, 1996; Fritsche *et al.*, 1993; Lauridsen and Danielsen, 2004; Peng *et al.*, 2010; Rooke *et al.*, 1998; Taugbøl *et al.*, 1993.

³ Includes C18:1n-7 and C18:1n-9; C18:1n-7 is approximately 5.5% of total C18:1.

Numerous studies have demonstrated that dietary sources of fat affect the proportion of fatty acids in colostrum and milk (see for examples Azain, 1993; DeMan and Bowland, 1963; Fritsche *et al.*, 1993; Lauridsen and Danielsen, 2004; Peng *et al.*, 2010; Rooke *et al.*, 1998; Schmid *et al.*, 2008; Taugbøl *et al.*, 1993; Yao *et al.*, 2012). Fatty acid composition of sow milk phospholipids was reported by Keenan *et al.* (1970). Chapter 16 (Bontempo and Jiang, 2015) of this book addresses the impact of various dietary fat sources on the neonatal piglet.

9.6.3 Other factors

In a comparison of European-derived breeds, Fahmy (1972) found that fat percentage in milk, but not in colostrum, is affected by breed. Yet, a later study comparing the Duroc and Landrace breeds, and selected and non-selected lines within each breed, showed no significant differences in milk fat content (Shurson and Irvin, 1992). Milk fat percentage is affected by genetic selection for sow cholesterol level, with low cholesterol sows having lower milk fat percentage than sows selected for high cholesterol (Kandeh *et al.*, 1993). Chinese Meishan sows have colostrum and milk that has higher fat content than Yorkshire (Zou *et al.*, 1992) or crossbred sows representing several breeds of European origin (Alston-Mills *et al.*, 2000). Meishan-derived sows also have more milk fat than Yorkshires on day 23 of lactation (Farmer *et al.*, 2001).

Colostrum fat percentage is significantly affected by colostrum yield, with higher percentages of fat being found in colostrum of low yield sows (Foisnet *et al.*, 2010a). Similarly, sow milk fat content appears to be negatively correlated with milk yield (White *et al.*, 1984), although other studies have not found an effect of milk yield on fat percentage (Garst *et al.*, 1999). Parity does not appear to affect fat percentage in sow colostrum, at least through parity 4 (Mahan and Peters, 2004). Results of the latter study also indicate that fat percentage in milk declines from parity 1 to parity 4. Peters and Mahan (2008) observed a quadratic effect of parity on milk fat between parity 1 and parity 6, with parities 3 and 4 having the lowest milk fat content. Goransson (1990) observed that fat percentage in colostrum of sixth parity sows was lower than that from first parity. Still, others have not observed a significant difference in milk fat content among parities (Baas *et al.*, 1992; Klobasa *et al.*, 1987). Increasing the number of piglets nursed is associated with a decrease in milk fat content at day 20 of lactation (Baas *et al.*, 1992), however, others have not observed an effect of litter size on fat percentage (Klobasa *et al.*, 1987). Milk fat content is not affected by body protein loss (Clowes *et al.*, 2003).

Studies that have evaluated the effect of environmental temperature on sow milk fat content have had variable results, with some showing a tendency for reduced fat percent when comparing 32 vs. 20 ° (Schoenherr *et al.*, 1989), but no effect when comparing 29 vs. 20 °C (Renaudeau and Noblet, 2001) or 30 vs. 20 °C (Prunier *et al.*, 1997). In that latter study, fat content of colostrum was also unaffected by ambient temperature. The fat content of sow milk is not affected by season (Shurson *et al.*, 1986).

9.7 Proteins

Proteins in mammary secretions are often determined indirectly by quantification of total nitrogen in the sample and then multiplying by an adjustment factor (such as $N\% \times 6.38$). Therefore, milk protein is usually reported as total protein or crude protein based on the nitrogen content of the sample. Mammary secretions contain other non-protein forms of nitrogen such as free amino acids, peptides, amino-sugars, and nucleotides.

9.7.1 Stage of lactation

Concentrations of total protein in sow mammary secretions are highest at parturition (Table 9.2). Similar protein concentrations are observed through 4 h after parturition, and then decline by over 50% by 24 h. These changes in total protein concentrations mirror the changes in immunoglobulin concentrations (discussed below). Total protein content of milk typically is in the 5.0 to 6.5% range (Table 9.3).

9.7.2 Other factors

Milk protein content generally is not affected by diet. Fahmy (1972) did not find an effect of sow breed on milk protein content, however, Shurson and Irvin (1992) did observe that Landrace sows have higher protein percentage than Duroc sows at day 21 of lactation. Zou *et al.* (1992) noted that Yorkshire sows have higher milk protein content at day 7 and day 21 than Meishan sows. However, comparison of milk from Meishan sows with crossbred sows representing several breeds of European origin does not show significant differences in milk protein content (Alston-Mills *et al.*, 2000) and milk protein content from 50% Meishan sows was similar to that of Yorkshire sows on day 23 of lactation (Farmer *et al.*, 2001). Total protein concentrations of sow milk are not affected by parity (Baas *et al.*, 1992; Goransson, 1990: Klobasa *et al.*, 1987).

9.7.3 Protein bound amino acids

Table 9.4 summarizes the average percentages of amino acids contained in the protein fraction of colostrum and milk. Glutamate accounts for 17 to 22% and proline 10 to 12% of the protein-bound amino acids. Branched chain amino acids (isoleucine, leucine and valine) collectively account for another 18 to 19% of the protein bound amino acids.

9.7.4 Major milk proteins

Estimates of the proportion of casein in total protein of colostrum at or immediately after parturition range from 9 to 32% (Brent *et al.*, 1973; Csapo *et al.*, 1996). The proportion of total protein that is casein increases to about 30 to 45% by 24 h postpartum during the period when immunoglobulin concentrations are significantly declining (Brent *et al.*, 1973; Csapo *et al.*, 1996). Most reports of casein content in sow milk are generally in the range of 50 to 55% of total protein throughout the remainder of lactation (Brent *et al.*, 1973; Csapo *et al.*, 1996; Mahan *et al.*, 1971; Richert *et al.*, 1997), however, higher

estimates have been reported in later lactation (Mahan *et al.*, 1971). The other major protein fraction of colostrum and milk are composed of the major whey proteins.

Total whey protein as a percentage of total protein in sow colostrum starts at 90% at the time of parturition, when immunoglobulins provide the major fraction of the whey protein, and then declines to approximately 70% at 24 h postpartum (Csapo *et al.*, 1996; Klobasa *et al.*, 1987). Total whey protein as a percentage of true protein is between 47 and 50% from day 10 through day 60 of lactation (Csapo *et al.*, 1996).

 β -lactoglobulin is the major whey protein in sow milk. Concentrations of β -lactoglobulin are relatively constant from the colostrum period through at least 7 days of lactation, ranging between 10 and 15 mg/ml (Hurley and Bryson, 1999; Jackson, 1990). α-lactalbumin concentrations are lowest in colostrum, at approximately 1.8 to 2.0 mg/ml, and gradually increase through the first 7 days of lactation to about 3.3 mg/ml (Hurley and Bryson, 1999; Jackson, 1990). Another whey protein in sow milk, whey acidic protein or cysteinerich whey protein, increases from approximately 0.3 mg/ml in colostrum to 0.9 mg/ml in milk from day 7 lactating sows (Hurley and Bryson, 1999; Jackson, 1990). Lactoferrin concentrations in colostrum at parturition are approximately 1.2 mg/ml, remain elevated through day 3 of lactation, and then decline to 0.3 mg/ml by day 7, followed by a continued slow decrease in concentration (Elliot et al., 1984). Concentrations of albumin in sow colostrum at parturition are 19 mg/ml, then decline to 8 mg/ml by 12 h postpartum, followed by a further gradual decline to stable concentrations of approximately 2.5 to 3.0 mg/ml during the second and third weeks of lactation (Klobasa and Butler, 1987). Zou et al. (1992) also noted several high molecular weight proteins in sow milk by protein gel analyses. Although these proteins were not identified, they seemed to segregate among breeds of pigs.

9.7.5 Immunoglobulins

The primary protein components of colostrum are the immunoglobulins, including the IgG, IgA and IgM isotypes (Hurley and Theil, 2013). Several subclasses of the IgG isotype have been characterized (Butler *et al.*, 2009), however, most studies determining colostrum and milk composition quantify total IgG in the secretion. Methods used to measure the immunoglobulins have ranged from the more classic immunoelectrophoresis and radial immunodiffusion techniques (Curtis and Bourne, 1971; Frenyo *et al.*, 1981; Jensen and Pedersen, 1979; Klobasa *et al.*, 1987) to the more recent use of enzyme-linked immunosorbent assays (ELISA; Foisnet *et al.*, 2010a,b, 2011; Jackson *et al.*, 1995; Loisel *et al.*, 2013; Markowska-Daniel and Pomorska-Mol, 2010; Quesnel *et al.*, 2008; Rolinec *et al.*, 2012).

Concentrations of immunoglobulins are highest in colostrum for the first several hours postpartum (Table 9.5). Immunoglobulin G, the major immunoglobulin in sow colostrum, continues at a high concentration for at least the initial 6 h postpartum. By 12 h, IgG concentrations have declined by nearly 50% compared with those at parturition, and they continue to decline to approximately 16% and 9% of levels determined at parturition by 24 and 48 h postpartum, respectively. Immunoglobulins A and M follow a similar pattern of

Table 9.5. Average and range of reported concentrations of immunoalobulins in sow colostrum and milk.

	Stage of lactation								
	0 h	6 h	12 h	24 h	48 h	72 h	12-45 d		
IgG (mg/ml) ¹									
Average ²	64.4	59.8	34.7	10.3	5.7	3.1	1.0		
Range ³	52-102	42-87	20-61	6-20	2-10	2-5	0.2-2.3		
Studies ⁴	12	7	5	11	6	6	4		
IgA (mg/ml)									
Average	13.1	11.4	9.3	5.0	3.8	4.1	4.0		
Range	5.5-24	8-17	7-13	1.5-9.2	2.7-4.5	3.6-4.5	1.9-6.6		
Studies	7	3	3	6	3	2	5		
IgM (mg/ml)									
Average	8.4	7.3	4.8	3.5	2.7	3.1	1.6		
Range	1.3-10.7	1.4 -5.9	1-9	1.8-4.5	1.8-4.5	1.7-4.5	0.9-2.4		
Studies	5	3	3	4	3	2	3		

¹ Total IgG.

declining concentrations during the initial day postpartum, although the decline in their concentrations occurs more slowly than for IgG (Table 9.5). Immunoglobulin A becomes the major immunoglobulin isotype present in milk by approximately day 3 of lactation.

Klobasa and Butler (1987) found that variability between individual sows in terms of immunoglobulin concentrations in mammary secretions was too high to identify significant differences other than for stage of lactation. No consistent differences were observed in comparisons across parities, and no statistically significant differences were found when comparing colostrum immunoglobulin concentrations among glands of the sow. Quesnel (2011) observed that immunoglobulin G concentrations in colostrum at parturition are not affected by parity, however IgG concentrations in sows with >5 parity are greater than for first parity sows at 24 h postpartum (Quesnel, 2011). Feed restriction of sows during the two weeks prepartum decreases colostrum IgA, but not IgG concentrations (Goransson, 1990).

9.7.6 Non-protein nitrogen

Non-protein nitrogen (NPN) fraction of milk includes free amino acids, nucleotides, amino sugars, and other nitrogen containing compounds. The total NPN fraction of milk typically is determined by precipitating the protein fraction with trichloroacetic acid,

² Average of values from studies that included mammary secretion sampling at the respective time relative to parturition.

³ Range of values from studies included in determining the average value.

⁴ Number of studies included in determining the average value. Studies used to estimate averages included: Curtis and Bourne, 1971; Foisnet *et al.*, 2010a,b, 2011; Frenyo *et al.*, 1981; Jackson *et al.*, 1995; Jensen and Pedersen, 1979; Klobasa *et al.*, 1987; Loisel *et al.*, 2013; Markowska-Daniel and Pomorska-Mol. 2010: Ouesnel *et al.*, 2008: Rolinec *et al.*, 2012.

filtering the supernatant and quantifying nitrogen in the supernatant using the Kjeldahl method (Csapo *et al.*, 1996; Klobasa *et al.*, 1987). Colostrum NPN is relatively low (64 mg N/100 g of colostrum; Csapo *et al.*, 1996). Content of NPN increases in milk through lactation, with reports ranging between 68 and 158 mg N/100 g of milk (Csapo *et al.*, 1996; Gurr, 1981; Klobasa *et al.*, 1987; Mahan *et al.*, 1971; Perrin, 1958; Sheffy *et al.*, 1952).

Wu and Knabe (1994) characterized free and protein bound amino acid concentrations in sow colostrum (collected 6 to 10 h postpartum) and milk (up to day 29 of lactation). Most free amino acids are found in the micromolar concentration range, in contrast to protein-bound amino acids that are in the millimolar range. The major free amino acids in colostrum are histidine, which subsequently decreases in concentration during lactation, and taurine, the concentration of which increases to day 8 of lactation and then remains constant. Most other free amino acids increase in concentration from colostrum to day 8 of lactation. Changes in concentrations of free amino acids between days 8 and 29 vary with the individual amino acid (Wu and Knabe, 1994). Total concentration of free non-essential amino acids is lowest in colostrum and increases through most of lactation, whereas the total concentration of free essential amino acids remains constant throughout lactation. Concentrations of urea increase from colostrum to day 3 of lactation and then decline to levels similar to those of colostrum (Wu and Knabe, 1994). Ammonia concentrations are highest in colostrum and then decline to day 8, and remain constant through the reminder of lactation (Wu and Knabe, 1994).

Nucleotide concentrations in sow colostrum change through lactation (Mateo *et al.*, 2004). For example, adenine 5'monophosphate follows a quadratic pattern with a peak at day 7 of lactation. However, uridine 5'monophosphate is highest at parturition and then declines through lactation (Atwood *et al.*, 1995; Mateo *et al.*, 2004). Concentrations of the polyamines, spermine and spermidine, increase from parturition to peak between 1 and 2 weeks of lactation and then decline as lactation progresses (Moytl *et al.*, 1995). Considerable individual variation is observed for concentrations of those polyamines. A number of nitrogen-containing sugars have also been identified in sow colostrum and milk (Tao *et al.*, 2010).

9.8 Energy

Gross energy of mammary secretions is estimated by combustion of the organic matter and quantification of the carbon dioxide released. Alternatively, some studies have estimated gross energy based on calculations using the content of organic components of milk (Laws et al., 2009). Detailed reports on gross energy of sow mammary secretions during the post-parturient period and throughout lactation are less prevalent than for other components (Table 9.2 and 9.3). Gross energy of colostrum at parturition is approximately 6.7 kJ/g and remains elevated at least through day 3 of lactation, before declining later in lactation. The relatively high level of gross energy estimated in colostrum at parturition is associated in part with the high concentration of immunoglobulins in colostrum. However, immunoglobulins tend to be more resistant to digestion than other milk proteins and contribute a smaller proportion of absorbed amino acids compared

with other whey proteins (Danielsen *et al.*, 2011; Yvon *et al.*, 1993). Estimates of gross energy based on bomb calorimetry may overestimate the energy that the piglet derives from colostrum. The transient increase in gross energy observed at day 2 and day 3 is likely associated with the peak in fat content that occurs during that phase of lactation.

9.9 Minerals

Total inorganic components of mammary secretions are typically reported as ash. From the summary of studies in Table 9.2 and 9.3, ash content of colostrum at parturition is approximately 0.68%. Ash percentage is increased by day 2 of lactation and then continues to increase gradually up to about week 2 and then remains at approximately 0.90%. The ash percentages reported in Table 9.3 for 42 to 60 d are based on a limited number of studies that have reported on this component during an extended lactation.

Table 9.6 summarizes reported concentrations of individual minerals in sow colostrum and milk. Concentrations of calcium are relatively low in colostrum, and then increase throughout lactation, at least up to week 6 or 7 of lactation (Coffey *et al.*, 1982; Gueguen and Salmon-Legagneur, 1959; Harmon *et al.*, 1974; Miller *et al.*, 1994; Perrin, 1955). Most, but not all, calcium is bound in the casein micelles. Concentrations of diffusible calcium are highest in colostrum and then decline as lactation progresses (Kent *et al.*, 1998), consistent with the concurrent increase in casein content. Phosphate concentrations follow a similar pattern to that of calcium, increasing in content from colostrum to milk (Table 9.6). Dietary level of calcium does not affect milk calcium concentration (Miller *et al.*, 1994), and an inorganic source of dietary microminerals results in higher milk calcium concentrations than an organic source (Peters *et al.*, 2010).

Concentrations of potassium and sodium are greater in colostrum than in milk (Table 9.6). Synthesis of most milk components occurs in the relatively high potassium and low sodium environment of the mammary epithelial cell. Therefore, mammary secretions reflect this potassium/sodium relationship. Chlorine is also found in greater amounts in colostrum than in milk (Table 9.6). Magnesium does not seem to be significantly different in concentration between colostrum and milk (Table 9.6). Sulfur content of colostrum is higher in colostrum than in milk (Table 9.6). Citrate is included here as an anion often associated with the diffusible calcium component. Concentrations of citrate decline from the colostrum phase to the milk phase (Holmes and Hartmann, 1993; Kent *et al.*, 1998 Konar *et al.*, 1971), consistent with the progression of lactogenesis and the increase in lactose as the major osmole in milk (Holmes and Hartmann, 1993; Peaker and Linzell, 1975).

Concentrations of microminerals in sow colostrum and milk are summarized in Table 9.6. Of particular note are copper, iron, iodine, manganese and zinc, each of which has a higher concentration in colostrum than in milk. Most studies have found that dietary level of iron does not affect iron concentration in mammary secretions (Pond and Jones, 1964; Pond *et al.*, 1965; Venn *et al.* 1947; Veum *et al.*, 1965), while other studies have observed an increased iron concentration in milk when sows are supplemented with iron

Table 9.6. Average and range of reported concentrations of macro- and microminerals in sow colostrum and milk.

	Colostrum ¹	l 	Milk		References ²
Macro-minerals	mg/ml	range	mg/ml (day) ³	range	
Ca	0.80	0.48-1.52	2.00 (d 9-28)	1.51-2.54	1, 3, 4, 6, 7, 8, 9, 11, 13, 16, 17, 18, 19
P	1.08	0.52-1.58	1.42 (d 9-28)	0.87-1.83	3, 4, 6, 7, 8, 9, 13, 16, 17, 18, 19
K	1.29	1.10-1.62	0.89 (d17-35)	0.36-1.57	3, 4, 6, 7, 11, 16, 17, 19
Na	0.83	0.68-1.00	0.42 (d 17-35)	0.33-0.54	3, 4, 6, 7, 11, 16, 17, 19
Cl	0.94	0.93-0.96	0.69 (d 16-35)	0.60-1.06	11, 18, 19
Citrate	1.70		0.94 (d 9-35)	0.77-1.19	9, 11
Mg	0.104	0.016-0.20	0.105 (d 9-28)	0.016-0.20	3, 4, 6, 7, 9, 16, 17, 18, 19
S	1.00		0.27 (d 17-21)	0.04-0.51	17, 19
Micro-minerals	μg/ml	range	μg/ml (day)	range	
Al	3.5		2.1 (d 20-21)	0.8-3.7	3, 16, 17
В	0.03		1.4 (g 20-21)	0.02-3.45	3, 16, 17
Cd	0.04		0.04 (d 21)		3
Cr	0.60		0.40 (d 20-21)	0.35-0.46	3, 16
Cu	1.80	0.26-3.77	0.92 (d 17-21)	0.12-2.01	3, 4, 16, 17, 19
Fe	2.84	1.7-5.4	1.96 (d 12-21)	1.27-4.6	2, 3, 4, 16, 19, 20, 24, 25
I	135		48 (d 23-27)	14-73	22, 23
Mn	0.26	0.06-0.45	0.15 (d 20-21)	0.06-0.36	3, 4, 16, 17
Мо	0.04		0.06 (d 20-21)	0.02-0.10	3, 17
Ni	0.42		0.31 (d 21)		3
Pb	0.17		0.16 (d 21)		3
Se	0.13	0.02-0.24	0.05 (d 14-28)	0.02-0.14	10, 12, 14, 15, 16, 19, 21, 26, 27
Sr	n/a		0.47 (d 21)		16
Zn	15.1	9.2-16.1	6.8 (d 17-35)	5.1-8.3	3, 4, 5, 16, 17, 19, 20

¹ Defined as within 12 h of parturition.

(Chaney and Barnhart, 1963; Earle and Stevenson, 1965). Milk concentration of copper is not affected by dietary level of the mineral, but is affected by source of microminerals (Peters *et al.*, 2010). Iodine concentrations in sow milk are increased with supplemental dietary iodine (Schone *et al.*, 1997, 2001).

² References: 1 = Alston-Mills *et al.*, 2000; 2 = Chaney and Barnhart, 1963; 3 = Coffey *et al.*, 1982; 4 = Csapo *et al.*, 1996; 5 = Earle and Stevensen, 1965; 6 = Elliott *et al.*, 1971; 7 = Fahmy, 1972; 8 = Harmon *et al.*, 1974; 9 = Kent *et al.*, 1998; 10 = Kim and Mahan, 2001; 11 = Konar *et al.*, 1971; 12 = Loudenslager *et al.*, 1986; 13 = Lyberg *et al.*, 2007; 14 = Mahan, 2000; 15 = Mahan *et al.*, 1977; 16 = Mahan and Newton, 1995; 17 = Park *et al.*, 1994; 18 = Perrin, 1955; 19 = Peters *et al.*, 2010; 20 = Pond *et al.*, 1965; 21 = Quesnel *et al.*, 2008; 22 = Schone *et al.*, 1997; 23 = Schone *et al.*, 2001; 24 = Venn *et al.*, 1947; 25 = Veum *et al.*, 1965; 26 = Yoon and McMillan, 2006; 27 = Zhan *et al.*, 2011.

³ Period in days of lactation when sows were sampled.

Selenium has been linked to innate and adaptive immune responses in animals (Salman et al., 2009). Concentrations of selenium are higher in colostrum than in milk (Table 9.6). The decline in selenium concentrations in mammary secretions occurs within the initial 2 to 3 d postpartum (Kim and Mahan, 2001; Loudenslager et al., 1986; Quesnel et al., 2008). Selenium concentrations in mammary secretions can be increased by dietary supplementation of the mineral, and organic forms of selenium used in supplementation of the diet are more effective at increasing colostrum and milk selenium concentrations than inorganic forms (Kim and Mahan, 2001; Mahan, 2000; Mahan and Peters, 2004; Quesnel et al., 2008; Yoon and McMillan, 2006; Zhan et al., 2011). Selenium concentrations in mammary secretions decline with increasing parity up to the fourth lactation, even when the diet is supplemented with inorganic forms of selenium (Mahan and Peters 2004). However, supplementation with organic selenium seems to counter this effect of parity on selenium concentrations in sow milk (Mahan and Peters 2004). Dietary supplementation of selenium to lactating sows may enhance the microbicidal activity of milk polymorphonuclear neutrophils (Wuryastuti et al., 1993).

9.10 Vitamins

Average concentrations of several vitamins in sow colostrum and milk are summarized in Table 9.7. Vitamin A concentration in sow colostrum (within the first 12 h after parturition) is high relative to milk. Estimates of vitamin A in colostrum range from 0.74 μ g/ml (using 1 I.U. = 0.3 μ g retinol; Braude *et al.*, 1946) to 1.81 μ g/ml (Elliott *et al.*, 1971). Concentration of vitamin A remains elevated through day 3 of lactation relative to concentrations later in lactation, corresponding to the increased fat content of mammary

Table 9.7. Average and range of reported concentrations of some vitamins in sow colostrum and milk.

	Colostrum ¹		Milk	References ²	
Vitamin	μg/ml	Range	μg/ml (day) ³	range	
A	1.14	0.474-1.81	0.48 (d 4-60)	0.15-0.92	1, 2, 3, 4, 5, 6, 7, 8, 10, 13, 14
D	0.015		0.006 (d 21-60)	0.003-0.009	4, 6
E	10.0	3.2-23.3	2.6 (d 16-60)	1.2-3.9	6, 12, 13, 14, 16, 17, 19
C	190	64-306	94 (d 15-60)	45-130	1, 2,6, 8, 9, 11
Thiamin	0.83	0.50-1.45	0.74 (d 10-56)	0.68-0.80	1, 2, 8, 18
Riboflavin	2.64	0.45-6.50	1.28 (d 10-56)	0.46-2.1	1, 2, 8, 18

¹ Defined as within 12 h of parturition.

² References: 1 = Bowland, 1966; 2 = Bowland *et al.*, 1951; 3 = Braude *et al.*, 1947; 4 = Braude *et al.*, 1946; 5 = Coffey *et al.*, 1982; 6 = Csapo *et al.*, 1996; 7 = Dever *et al.*, 2011; 8 = Elliott *et al.*, 1971; 9 = Heidebrecht *et al.*, 1951; 10 = Heying *et al.*, 2013; 11 = Hidiroglou and Batra, 1995; 12 = Lauridsen and Danielsen, 2004; 13 = Lauridsen *et al.*, 2002; 14 = Lauridsen and Jensen, 2005; 15 = Loudenslager *et al.*, 1986; 16 = Mahan, 1991; 17 = Mahan *et al.*, 2000; 18 = Neuhaus, 1961; 19 = Pinelli-Saavedra *et al.*, 2008.

³ Inclusive period of lactation from which reported data was used to calculate the average concentration.

secretions during that time. Estimates of vitamin A concentration in milk from day 5 through day 28 range from 0.14 to 0.73 µg/ml. Reports of vitamin A concentrations in a lactation extended beyond day 28 have presented widely variable results (Csapo et al., 1996; Heidebrecth et al., 1951). Content of vitamin A in colostrum and milk is affected by the vitamin level and source in the diet. Feeding sows orange corn vs. white corn during gestation and lactation increases milk retinol concentration (Heying et al. 2013). Supplementation of late gestation and lactation diets with fish oil, but not with animal fat or various other oils, increases vitamin A concentration in sow milk (Lauridsen and Danielsen, 2004). On the other hand, others have shown that feeding animal fat during late gestation and lactation increases vitamin A concentrations in colostrum and milk compared with a basal diet (Coffey et al., 1982). Braude et al. (1946, 1947) reported a greater vitamin A concentration in sow milk during summer than in winter, most likely attributable to summer housing of sows on pasture after the first week of lactation, in contrast to winter indoor housing from about 2 weeks prepartum through lactation. Oral dosing of a lactating sow with retinol results in elevated milk retinol that peaks at 7.5 to 10 h post-dosing (Dever et al., 2011).

Vitamin E concentrations reported in colostrum during the initial day of parturition range from 3.2 to 23.3 µg/ml, with an average of 10 µg/ml (Table 9.7). By day 2, vitamin E concentrations are 3.7 to 7.7 μg/ml (Csapo et al., 1996; Lauridsen and Jensen, 2005; Lauridsen et al., 2002). Sow milk from day 16 to day 60 of lactation has a vitamin E content averaging 2.6 µg/ml (Table 9.7). Most studies report a significant effect of stage of lactation on vitamin E concentrations in mammary secretions (Lauridsen and Danielsen, 2004; Lauridsen and Jensen, 2005; Lauridsen et al., 2002; Mahan, 1991; Mahan et al., 2000; Malm et al., 1976; Pinelli-Saavedra et al., 2008). Dietary supplementation of gestation and/or lactation diets with vitamin E increases colostrum and milk vitamin E content (Lauridsen and Jensen, 2005; Mahan, 1991; Mahan et al., 2000; Malm et al., 1976; Pinelli-Saavedra et al., 2008). Supplementation of late gestation and lactation diets with coconut oil increases vitamin E concentration in sow milk relative to supplementation with animal fat or various other oils (Lauridsen and Danielsen, 2004). Mahan et al. (2000) found a quadratic effect of parity on vitamin E, with highest concentrations in parities 2 and 3. Limited information is available on vitamin D (Table 9.7) and vitamin K in sow milk. Concentrations of vitamin D are highest in colostrum at parturition, at about 0.015 μg/ml, and then are approximately 0.006 μg/ml in later lactation (Bowland et al., 1951; Csapo et al., 1996). Vitamin K concentrations range from 0.089 µg/ml to 0.101 µg/ml, but do not seem to be affected by stage of lactation (Csapo et al., 1996).

Vitamin C concentration is highest in colostrum vs. milk, with values ranging between 64 and 306 µg/ml, and averaging 190 µg/ml (Table 9.7). Concentrations of vitamin C in milk average 94 µg/ml, and range from 45 to 130 µg/ml (Table 9.7). Information on the B vitamins in sow colostrum and milk is also limited. Thiamine (B1) in colostrum has been reported as ranging from 0.5 to 1.45 µg/ml and averages 0.83 µg/ml, while milk thiamine averages 0.74 µg/ml, with reports ranging from 0.7 to 0.8 µg/ml (Table 9.6). Thiamine in milk is affected by season, with lower concentrations in summer when sows were housed outdoors on pasture through most of lactation (Braude *et al.*, 1947). In contrast to most other vitamins, thiamine concentrations do not appear to be greater in colostrum than in

milk (Elliott *et al.*, 1971). Reports of riboflavin (B2) in colostrum range from 0.45 to 6.5 μ g/ml and average 2.6 μ g/ml (Table 9.6). Milk riboflavin concentration is approximately 1.28 μ g/ml and reports range from 0.4 to 8.2 μ g/ml (Table 9.6). Riboflavin concentration appears to be higher in colostrum than in milk (Elliott *et al.*, 1971). Neither thiamine nor riboflavin concentrations are affected by level of dietary protein (up to 15%; Elliott *et al.*, 1971).

In a review of the literature from 1930 to 1961, Neuhaus (1961) reported colostrum concentrations of niacin at approximately 1.65 µg/ml and of pantothenic acid ranging from 1.3 to 6.8 µg/ml. Vitamin B6 in sow milk (Coburn *et al.*, 1992; stage of lactation not reported) includes 101, 563, and 45 ng/ml, respectively of pyridoxal, pyridoxal 5'-phosphate, and pyridoxamine 5'-phosphate, which are considerably higher levels than the 25 ng/ml of vitamin B6 reported for colostrum (Neuhaus, 1961). Biotin concentrations in colostrum are approximately 53 ng/ml (Neuhaus, 1961), and in milk at day 14 of lactation, they are 24 to 68 ng/ml (Bryant *et al.*, 1985). Bryant *et al.* (1985) observed that milk biotin concentrations are increased in sows receiving supplemental dietary biotin.

Folate (B) in colostrum (values taken from day 1 data) has been reported at 13 to 44 ng/ml (Barkow *et al.*, 2001; Ford *et al.*, 1975; O'Connor *et al.*, 1989). Concentrations of folate then decline by 50 to 60% by day 7 of lactation (Ford *et al.*, 1975; Matte and Girard, 1989). Reports of folate concentrations at 16 to 28 d of lactation range from 2.3 to 13.4 ng/ml (Barkow *et al.*, 2001; Ford *et al.*, 1975; Matte and Girard, 1989; O'Connor *et al.*, 1989). Milk folate concentrations can be increased through dietary supplementation (Barkow *et al.*, 2001) or weekly intramuscular folic acid injections (Matte and Girard, 1989). Cobalamin (B) in colostrum is approximately 1.5 ng/ml (Ford *et al.*, 1975; Neuhaus, 1961). Ford *et al.* (1975) also quantified cobalamin in sow milk from day 7 through day 49 of lactation. Cobalamin concentrations were highest at day 14 (2.41 ng/ml) and then ranged from 1.40 to 1.64 ng/ml through the remainder of lactation.

9.11 Cells

Total somatic cell concentration in milk is referred to as somatic cell count (SCC). Reported estimates of SCC for sow milk have varied considerably. Some authors observed SSC in early lactation (typically reported as day 1 or 2 of lactation) that ranged from 5.3×10⁵ cells/ml (Hurley and Grieve, 1988) to 1.06×10⁶ cells/ml (Schollenberger *et al.*, 1986a), and up to 8×10⁶ cells/ml (Garst *et al.*, 1999). Evans *et al.* (1982) reported colostrum SSC ranging from 2×10⁵ to 5×10⁷ cells/ml (mean=1×10⁷), and Osterlundh *et al.* (1998) reported 7.9×10⁶ polymorphonuclear neutrophils/ml. Observed changes in SSC during lactation also varied among reports. Osterlundh *et al.* (1998) found that the concentration of polymorphonuclear neutrophils significantly decreased between days 1 and 3 of lactation. Garst *et al.* (1999) reported that SCC increased linearly from day 2 to day 51 of lactation. Schollenberger *et al.* (1986a) only found SSC to be significantly elevated at days 8 to 14 compared with colostrum SSC and did not observe a correlation between SSC and day of lactation. Others observed no significant change in SCC from the first day of lactation through day 28 (Hurley and Grieve, 1988). Reports of SSC at

days 8 to 14 have ranged from 2.9×10^5 cells/ml (Hurley and Grieve, 1988), up to 8.5×10^6 cells/ml (Garst *et al.*, 1999), with others reporting 1 to 2×10^6 cells/ml (Evans *et al.*, 1982; Schollenberger *et al.*, 1986a).

The differences in reported SSC in sow colostrum and milk may arise from several sources. Subclinical mastitis in dairy cattle is often determined by observing an associated increase in SSC in the absence of clinical symptoms. An elevated SSC would be expected in the case of either clinical or subclinical mastitis in the sow. The presence of subclinical mastitis often is not accounted for in studies evaluating SCC in swine. The route of oxytocin administration for milk collection also affects SCC, with intramuscular administration resulting in higher SCC than intravenous administration (Garst et al., 1999). Others have reported that hind milk, the milk removed by oxytocin administration after piglets have suckled, is higher in total solid and milk fat (Atwood and Hartmann, 1992). A similar variation in SCC among fractions of milk removed has been reported in cow milk (Paape and Tucker, 1966). Incomplete removal of milk from the sow's glands may therefore result in underestimated estimates of SSC. In addition, different methods have been used to determine SSC, including direct microscopic cell count (Evans et al., 1982; Hurley and Grieve, 1988) or analysis of milk samples by a dairy herd improvement laboratory primarily used for dairy cattle milk analyses (Garst et al., 1999). Milk cells often are collected by centrifugation of milk samples and evaluation of the resulting cell pellet. However, cells are also found in the fat or cream fraction of milk that has been centrifuged (Phipps and Newbould, 1966), and care should be taken to account for this portion in estimates of SSC.

Milk cells include several leukocyte types, including neutrophils, macrophages, lymphocytes, and eosinophils, as well as epithelial cells (Lee *et al.*, 1983; Le Jan, 1995; Schollenberger *et al.*, 1986b,c). Table 9.8 summarizes the average differential cell count of sow colostrum and milk based on studies that distinguished all five cell types. Neutrophils are the major cell type at all stages of lactation. Highest concentrations of

	Colostrum ²		Milk (days 3-7)		Milk (days 1	4-21)
Cell type	%	Range	%	Range	%	Range
Neutrophils	64.9	61.2-71.1	47.9	40.7-55.4	41.1	28.2-51.3
Macrophages	9.5	1.3-24.5	12.0	8.6-15.5	11.0	5.5-16.3
Lymphocytes	18.1	8.8-26.5	15.3	7.9-22.8	9.8	6.0-12.2
Eosinophils	0.7	0.2-1.5	1.5	0.4-2.6	0.8	0.2-1.5
Epithelial	6.0	0.4-19.6	23.2	6.1-36.8	37.3	31.3-48.0

¹ References used for determining average differential cell count: Evans *et al.,* 1982; Lee *et al.,* 1983; Schollenberger *et al.,* 1986a; Wuryastuti *et al.,* 1993.

² Within 2 d of parturition.

neutrophils are observed in colostrum, followed by declining neutrophil concentrations as lactation progresses. Greater variability of reported neutrophil concentrations is observed later in lactation. Average concentrations of macrophages and lymphocytes are relatively constant throughout lactation, however, considerable variability exists among reported differential cell counts. Eosinophils on average make up less than 2% of total cells in mammary secretions. Proportions of epithelial cells change dramatically during lactation, with low percentages observed in colostrum, followed by a rapid increase after the colostrum phase. Weaning results in mammary secretions with 90 to 98% neutrophils (Lee *et al.*, 1983).

9.12 Bioactive components

Colostrum and milk contain a wide array of biologically active factors, including immunoglobulins and leukocytes (discussed above), enzymes, hormones and growth factors, and others. Some of these components are briefly discussed here for sow colostrum and milk.

Many hormones, growth factors and cytokines have been identified in milk of various species (Baumrucker and Magliaro-Macrina, 2011; Pakkanen and Aalto, 1997). Many of these biologically active components are thought to have effects in the neonate. Concentrations of prolactin in colostrum are highest just prior to parturition and decline rapidly during the first 24 h postpartum (Devillers *et al.*, 2004a). After the colostrum period, prolactin slowly declines from about day 5 through the remainder of lactation (Mulloy and Malven, 1979). Milk prolactin concentrations are affected by litter size, with sows nursing litters of 8 piglets having lower milk prolactin concentrations compared with sows nursing litters of 10 or 12 piglets (Mulloy and Malven, 1979). Concentrations of serum prolactin and milk prolactin are positively correlated at least through day 13 of lactation (Mulloy and Malven, 1979).

Relaxin is also found in sow milk (Yan *et al.*, 2006), secreted as the pro-form of the hormone (Bagnell *et al.*, 2009). Concentrations of relaxin are highest in colostrum and then decline over the first 4 to 6 d of lactation (Yan *et al.*, 2006). This milk-borne relaxin is thought to be a route of maternal programming of neonatal development in the lactocrine hypothesis (Bagnell *et al.*, 2009).

Concentrations of leptin in defatted mammary secretions decrease from parturition to day 7 of lactation, and then remain unchanged through 22 d of lactation (Estienne *et al.*, 2000). However, leptin concentrations in whole milk are not affected by stage of lactation (Estienne *et al.*, 2000). Neither whole nor skim milk leptin concentrations are significantly affected by body condition, and they are not correlated with backfat thickness or sow serum leptin concentration (Estienne *et al.*, 2000). Mean leptin concentrations in mammary secretions during the initial 4 d of lactation are significantly greater in Yorkshire (75%) × Meishan (25%) crossbred sows than in Meishan sows (Mostyn *et al.*, 2006).

Sow colostrum and milk contain several steroid hormones. The mammary gland of the sow produces estradiol, a function that seems to be under the control of progesterone (Staszkiewicz et al., 2004). Estradiol concentrations in the sow's plasma are elevated prior to parturition and decline rapidly during the initial day postpartum (Devillers et al., 2004a; Osterlundh et al., 1998). Concentrations of estradiol in whole colostrum collected just prior to parturition are 3 to 4 fold greater than in plasma at the same period (Devillers et al., 2004a). In another study using fat-free colostrum, concentrations of estradiol were about half the plasma concentrations (Osterlundh et al., 1998). Estradiol concentrations decline rapidly during the first day postpartum from about 1.5 ng/ml at parturition to 0.5 ng/ml by 24 h postpartum (Devillers et al., 2004a). Concentrations of estrone in whole sow colostrum are highest immediately after parturition (13.8 ng/ml) and rapidly decline over the first 24 h, reaching 0.5 ng/ml by 48 h postpartum (Farmer et al., 1987). Estrone concentrations in whole sow mammary secretions are not affected by gland location (Farmer et al., 1987). Concentrations of progesterone in sow mammary secretions follow a similar pattern to that of estrogens, with concentrations being highest in colostrum and then rapidly declining during the initial day postpartum (Devillers et al., 2004a). Cortisol is also present in sow mammary secretions, with highest concentrations approximately 2 to 2.5 fold greater shortly after parturition compared with milk concentrations (measured in fat-free secretion; Osterlundh et al., 1998).

Concentrations of insulin and neurotensin are elevated in colostrum at parturition and then decline over the initial 3 d of lactation, while concentrations of bombesin remain relatively constant through the same period (Westrom *et al.*, 1987). Concentrations of thyroid hormones in milk do not appear to be different between colostrum and milk during early lactation (Mostyn *et al.*, 2006). A breed effect has been noted for triiodothyronine concentrations in sow mammary secretions, but not for thyroxine (Mostyn *et al.*, 2006).

Several growth factors and growth-factor activities have been identified in sow milk. Concentrations of insulin-like growth factor-I (IGF-I) are highest in colostrum collected during the first day postpartum (ranging from 14 to 70 ng/ml), then decline by more than 50% by the second day postpartum, and continue declining through about day 10 of lactation (ranging from 3 to 14 ng/ml; Monaco et al., 2005). The effect of stage of lactation is significant on IGF-I concentrations in sow mammary secretions, while there is no significant difference between first and second parities (Monaco et al., 2005). Simmen et al. (1990) also observed an effect of stage of lactation on IGF-I concentrations in mammary secretions, as well as a breed effect. An epidermal growth factor-like peptide has been identified in sow milk (Tan et al., 1990). Epidermal growth factor concentrations, estimated by radioreceptor assay, are highest in mammary secretions collected in the first 24 h postpartum, decline by ~90% by day 9 of lactation, and then remain relatively constant at least through day 27 (Jaeger et al., 1987). Prostaglandin-like activity declines approximately 2.5 fold from the high levels in colostrum to day 5 of lactation and remains constant at least through day 20 of lactation (Maffeo et al., 1987). A number of 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 (Nguyen *et al.*, 2007). Each cytokine identified has the highest concentrations in colostrum and early lactation milk, followed by declining concentrations as lactation progresses, although declining at differing rates (Nguyen et al., 2007).

Chandan *et al.* (1968) found lipase and ribonuclease activity in sow milk, but not lysozyme activity. Krakowski *et al.* (2002) reported lysozyme activity of 15 to 20 ng/ml in sow colostrum immediately after parturition. Trypsin inhibitor activity has been identified in sow colostrum (Jensen, 1978). Ceruloplasmin concentrations in sow milk are higher at day 3 compared with day 33 of lactation (Cerveza *et al.*, 2000).

9.13 Effects of physiological state

The initiation of lactation, known as lactogenesis, has been described as occurring in two phases (Hartmann, 1973). The initial phase involves structural and enzymatic differentiation of the mammary cells preparing them for secretion of milk. This phase coincides with colostrum formation. In the sow, this phase of lactogenesis is occurring during the late stages of gestation (Kensinger et al., 1982). The second phase of lactogenesis, referred to as copious milk secretion, coincides with a rapid increase in secretion volume, which may not fully begin until 33 to 34 h postpartum in the sow (Krogh et al., 2012; Theil et al., 2014). Natural variability is observed in the physiological coordination between parturition and progression through the stages of lactogenesis. For example, sows with low volume production of mammary secretions during the initial 24 h after the onset of farrowing, as determined by piglet body weight variation, had greater total solids, fat and gross energy contents, but lower lactose content of colostrum at parturition than sows with high colostrum production (Foisnet et al., 2010a). This suggests that sows with low colostrum production were not as far advanced in the process of lactogenesis at the time of parturition as the high colostrum-producing sows. Total solids content of mammary secretions at 24 h postpartum is not different between low and high colostrum producing sows (Foisnet et al., 2010a).

A misalignment of the timing of parturition and lactogenesis is also seen in studies where parturition is hormonally manipulated to occur earlier or later than normal. Induction of parturition to occur prior to day 114 of gestation can decrease fat content of colostrum secretions, while lactose concentration in colostrum is not affected by induced early parturition (Jackson *et al.*, 1995). Sows treated on day 113 of gestation to induce parturition at day 114 have higher lactose content, lower protein and ash content and tend to have lower total solids content of colostrum at parturition than sows not induced (Foisnet *et al.*, 2011). On the other hand, delaying parturition of sows to day 116 with a progestogen does not affect total solids, lactose, fat, protein or ash content of colostrum at parturition or at 24 h (Jackson *et al.*, 1995; Foisnet *et al.*, 2010b), however total solids and gross energy percentages are decreased at 48 h postpartum (Foisnet *et al.*, 2010b).

Altering the lactogenic process through transgenic modification of mammary cell function can also alter colostrum composition. In transgenic first lactation sows expressing the bovine α -lactalbumin gene, total solids in colostrum within 6 h of farrowing are lower than in non-transgenic sows (Noble *et al.*, 2002). Lactose content of colostrum from transgenic sows is higher than in non-transgenic sows, suggesting that the process of lactogenesis, indicated here through lactose synthesis, was more advanced in the

transgenic sows. The increased lactose synthesis would result in a greater water volume diluting the other colostrum components (Noble *et al.*, 2002).

9.14 Conclusions

The composition of sow mammary secretions is most dramatically affected by stage of lactation. Mammary secretions from the initial 24 h after parturition are considered as colostrum. Compared with mature milk, colostrum has high concentrations of protein, particularly immunoglobulins, some microminerals (particularly copper, iron, iodine, and zinc), some vitamins, and hormones and growth factors. Lactose is present in lower concentrations in colostrum than in mature milk. Milk fat concentration transiently increases during the period from day 2 to day 4. The composition of milk after approximately day 7 to day 10 is relatively stable for the remainder of lactation. Diet can affect some milk components, including concentrations of fat, fat-soluble vitamins and some minerals, as well as proportions of specific fatty acids. Some components of sow milk also are affected by genetics, parity, colostrum and milk yield, and ambient temperature.

References

- Alston-Mills, B., Iverson, S.J. and Thompson, M.P., 2000. A comparison of the composition of milks from Meishan and crossbred pigs. Livestock Production Science 63: 85-91.
- Ariza-Nieto, C., Bandrick, M., Baidoo, S.K., Anil, L., Molitor, T.W. and Hathway, M.R., 2011. Effect of dietary supplementation of oregano essential oils to sows on colostrum and milk composition, growth pattern and immune status of suckling pigs. Journal of Animal Science 89: 1079-1089.
- Atwood, C.S. and Hartmann, P.E., 1992. Collection of fore and hind milk from the sow and the changes in milk composition during suckling. Journal of Dairy Research 59: 287-298.
- Atwood, C.S., Toussaint, J.K. and Hartmann, P.E., 1995. Assessment of mammary gland metabolism in the sow. II. Cellular metabolites in the mammary secretion and plasma during lactogenesis II. Journal of Dairy Research 62: 207-220.
- Azain, M.J., 1993. Effects of adding medium-chain triglycerides to sow diets during late gestation and early lactation on litter performance. Journal of Animal Science 71: 3011-3019.
- Baas, T.J., Christian, L.L. and Rothschild, M.F., 1992. Heterosis and recombination effects in Hampshire and Landrace swine: I. Maternal traits. Journal of Animal Science 70: 89-98.
- Bagnell, C.A., Steinetz, B.G. and Bartol, F.F., 2009. Milk-borne relaxin and the lactocrine hypothesis for maternal programming of neonatal tissues. Annals of the New York Academy of Science 1160: 152-157.
- Barkow, B., Matte, J.J., Bohme, H. and Flachowsky, G., 2001. Influence of folic acid supplements on the carry-over of folates from sow to the piglet. British Journal of Nutrition 85: 179-184.
- Baumrucker, C.R. and Magliaro-Macrina, A.L., 2011. Hormones in milk. Encyclopedia of Dairy Sciences (2nd ed.), pp. 765-771.
- Bontempo, V. and Jiang, X.R., 2015. Feeding various fat sources to sows: effects on immune status and performance of sows and piglets. Chapter 16. In: Farmer, C. (ed.) The gestating and lactating sow. Wageningen Academic Publishers, Wageningen, the Netherlands, pp. 357-375.

- Bowland J.P., Grummer, R.H., Phillips, P.H. and Bohstedt, G., 1951. Seasonal variation in the fat, vitamin A, and vitamin D content of sows colostrum and milk. Journal of Animal Science 10: 533-537.
- Bowland, J.P., 1966. Swine milk composition a summary. In: Bustad, L.K. and McClellan, R.O. (eds.) Swine in biomedical research. Pacific Northwest National, Richland, Washington, DC, USA, pp. 97-107.
- Boyd, R.D., Moser, B.D., Peo, Jr., E.R., Lewis, A.J. and Johnson, R.K., 1982. Effect of tallow and choline chloride addition to the diet of sows on milk composition, milk yield and preweaning pig performance. Journal of Animal Science 54: 1-7.
- Braude, R., Coates, M.E., Henry, K.M., Kon, S.K., Rowland, S.J., Thompson, S.Y. and Walker, D.M., 1947. A study of the composition of sow's milk. British Journal of Nutrition 1: 64-77.
- Braude, R., Kon, S.K. and Thompson, S.Y., 1946. A note on certain vitamins of sow's colostrum. Journal of Dairy Research 14: 414-418.
- Brent, B.E., Miller, E.R., Ullrey, D.E. and Kemp, K.E., 1973. Postpartum changes in nitrogenous constituents of sow milk. Journal of Animal Science 36: 73-78.
- Brooks, P.H. and Burke, J., 1998. Behaviour of sows and piglets during lactation. In: Verstegen, M.W.A., Moughan, P.J. and Schrama, J.W. (eds.) The lactating sow. Wageningen Pers, Wageningen, the Netherlands, pp. 301-338.
- Bryant, K.L., Kornegay, E.T., Knight, J.W., Webb, Jr., K.E. and Notter, D.R., 1985. Supplemental biotin for swine. II. Influence of supplementation to corn- and wheat-based diets on reproductive performance and various biochemical criteria of sows during four parities. Journal of Animal Science 60: 145-153.
- Butler, J.E., Wertz, N., Deschacht, N. and Kacskovics, I., 2009. Porcine IgG: structure, genetics, and evolution. Immunogenetics 61: 209-230.
- Cerveza, P.J., Mehrbod, F., Cotton, S.J., Lomeli, N., Linder, M.C., Fonda, E.G. and Wickler, S.J., 2000. Milk ceruloplasmin and its expression by mammary gland and liver in pigs. Archives of Biochemistry and Biophysics 373: 451-461.
- Chandan, R.C., Parry, Jr., R.M. and Shahani, K.M., 1968. Lysozyme, lipase, and ribonuclease in milk of various species. Journal of Dairy Science 51: 606-607.
- Chaney, C.H. and Barnhart, C.E., 1963. Effect of iron supplementation of sow rations on the prevention of baby pig anemia. Journal of Nutrition 81: 187-192.
- Clowes, E.J., Aherne, F.X., Foxcroft, G.R. and Baracos, V.E., 2003. Selective protein loss in lactating sows is associated with reduced litter growth and ovarian function. Journal of Animal Science 81: 753-764.
- Coburn, S.P., Mahuren, J.D., Pauly, T.A., Ericson, K.L. and Townsend, D.W., 1992. Alkaline phosphatase activity and pyridoxal phosphate concentrations in the milk of various species. Journal of Nutrition 122: 2348-2353.
- Coffey, M.T., Seerley, R.W. and Mabry, J.W., 1982. The effect of source of supplemental dietary energy on sow milk yield, milk composition and litter performance. Journal of Animal Science 55: 1388-1394.
- Coffey, M.T., Yates, J.A. and Combs, G.E., 1987. Effects of feeding sows fat or fructose during late gestation and lactation. Journal of Animal Science 65: 1249-1256.
- Csapo, J., Martin, T.G., Csapo-Kiss, Z.S. and Hazas, Z., 1996. Protein, fats, vitamin and mineral concentrations in porcine colostrum and milk from parturition to 60 days. International Dairy Journal 6: 881-902.

- Curtis, J. and Bourne, F.J., 1971. Immunoglobulin quantitation in sow serum, colostrum and milk and the serum of young pigs. Biochimica et Biophysica Acta 236: 319-332.
- Danielsen, M., Pedersen, L.J. and Bendixen, E., 2011. An *in vivo* characterization of colostrum protein uptake in porcine during early lactation. Journal of Proteomics 74: 101-109.
- Darragh, A.J. and Moughan, P.J., 1998. The composition of colostrum and milk. In: Verstegen, M.W.A., Moughan, P.J. and Schrama, J.W. (eds.) The lactating sow. Wageningen Pers, Wageningen, the Netherlands, pp. 3-21.
- De Quelen, F., Boudry, G. and Mourot, J., 2010. Linseed oil in the maternal diet increases long chain-PUFA status of the foetus and the newborn during the suckling period in pigs. British Journal of Nutrition 104: 533-543.
- De Quelen, F., Boudry, G. and Mourot, J., 2013. Effect of different contents of extruded linseed in the sow diet on piglet fatty acid composition and hepatic desaturase expression during the post-natal period. Animal 7: 1671-1680.
- DeMan, J.M. and Bowland, J.P., 1963. Fatty acid composition of sow's colostrum, milk and body fat as determined by gas-liquid chromatography. Journal of Dairy Research 30: 339-343.
- Den Hartog, L.A., Boer, H., Bosch, M.W., Klaassen, G.J. and Van der Steen, H.A.M., 1987. The effect of feeding level, stage of lactation and method of milk sampling on the composition of milk (fat) in sows. Journal of Animal Physiology and Animal Nutrition 58: 253-261.
- DeRouchey, J.M., Hancock J.D., Hines, R.H., Cummings, K.R., Lee, D.J., Maloney, C.A., Dean, D.W., Park, J.S. and Cao, H., 2003. Effects of dietary electrolyte balance on the chemistry of blood and urine in lactating sows and sow litter performance. Journal of Animal Science 81: 3067-3074.
- Dever, J.T., Surles, R.L., Davis, C.R. and Tanumihardjo, S.A., 2011. α-Retinol is distributed through serum retinol-binding protein-independent mechanisms in the lactating sow-nursing piglet dyad. Journal of Nutrition 141: 42-47.
- Devillers, N., Farmer, C. Mounier, A.M., Le Dividich, J. and Prunier, A., 2004a. Hormones, IgG and lactose changes around parturition in plasma, and colostrum or saliva of multiparous sows. Reproduction Nutrition Development 44: 381-396.
- Devillers, N., Van Milgen, J., Prunier, A. and Le Dividich, J., 2004b. Estimation of colostrum intake in the neonatal pig. Animal Science 78: 305-313.
- Dourmad, J.Y., Noblet, J. and Etienne, M., 1998. Effect of protein and lysine supply on performance, nitrogen balance, and body composition changes of sows during lactation. Journal of Animal Science 76: 542-550.
- Dunshea, F.R., Bauman, D.E., Nugent, E.A., Kerton, D.J., King, R.H. and McCauley, I., 2005. Hyperinsulinaemia, supplemental protein and branched-chain amino acids when combined can increase milk protein yield in lactating sows. British Journal of Nutrition 93: 325-332.
- Earle, I.P. and Stevensen, J.W., 1965. Relation of dietary zinc to composition of sow colostrum and milk. Journal of Animal Science 24: 325-328.
- Elliot, J.L., Senft, B., Erhardt, G. and Fraser, D., 1984. Isolation of lactoferrin and its concentration in sows' colostrum and milk during a 21-day lactation. Journal of Animal Science 59: 1080-1084.
- Elliott, R.F., Vander Noot, G.W., Gilbreath, R.L. and Fisher, H., 1971. Effect of dietary protein level on composition changes in sow colostrum and milk. Journal of Animal Science 32: 1128-1137.
- Estienne, M.J., Harper, A.F., Barb, C.R. and Azain, M.J., 2000. Concentrations of leptin in serum and milk collected from lactating sows differing in body condition. Domestic Animal Endocrinology 19: 275-280.

- Evans, P.A., Newby, T.J., Stokes, C.R. and Bourne, F.J., 1982. A study of cells in the mammary secretions of sows. Veterinary Immunology and Immunopathology 3: 515-527.
- Fahmy, M.H., 1972. Comparative study of colostrum and milk composition of seven breeds of swine. Canadian Journal of Animal Science 52: 621-627.
- Farmer, C., Giguère, A. and Lessard, M., 2010. Dietary supplementation with different forms of flax in late gestation and lactation: effects on sow and litter performances, endocrinology, and immune response. Journal of Animal Science 88: 225-237.
- Farmer, C., Houtz, S.K. and Hagen, D.R., 1987. Estrone concentration in sow milk during and after parturition. Journal of Animal Science 64: 1086-1089.
- Farmer, C., Palin, M.F., Sorensen, M.T. and Robert, S., 2001. Lactational performance, nursing and maternal behavior of Upton-Meishan and large white sows. Canadian Journal of Animal Science 81: 487-493.
- Flummer, C. and Theil, P.K., 2012. Effect of β -hydroxy β -methyl butyrate supplementation of sows in late gestation and lactation on sow production of colostrum and milk and piglet performance. Journal of Animal Science 90: 372-374.
- Foisnet, A., Farmer, C., David, C. and Quesnel, H., 2010a. Relationships between colostrum production by primiparous sows and sow physiology around parturition. Journal of Animal Science 88: 1672-1683.
- Foisnet, A., Farmer, C., David, C. and Quesnel, H., 2010b. Altrenogest treatment during late pregnancy did not reduce colostrum yield in primiparous sows. Journal of Animal Science 88: 1684-1693.
- Foisnet, A., Farmer, C., David, C. and Quesnel, H., 2011. Farrowing induction induces transient alterations in prolactin concentrations and colostrum composition in primiparous sows. Journal of Animal Science 89: 3048-3059.
- Ford, J.E., Scott, K.J., Sansom, B.F. and Taylor, P.J., 1975. Some observations on the possible significance of vitamin B12- and folate-binding proteins in milk. Absorption of [58Co] cyanocobalamin by sucking piglets. British Journal of Nutrition 34: 469-492.
- Frenyo, V.L., Peters, G., Antal, T. and Szabo, I., 1981. Changes in colostral and serum IgG content in swine in relation to time. Veterinary Research Communications 4: 275-282.
- Fritsche, K.L., Huang, S.C. and Cassity, N.A., 1993. Enrichment of omega-3 fatty acids in suckling pigs by maternal dietary fish oil supplementation. Journal of Animal Science 71: 1841-1847.
- Garst, A.S., Ball, S.F., Williams, B.L., Wood, C.M., Knight, J.W., Moll, H.D., Aardema, C.H. and Gwazdauskas, F.C., 1999. Influence of pig substitution on milk yield, litter weights, and milk composition of machine milked sows. Journal of Animal Science 77: 1624-1630.
- Gaucheron, F., 2005. The minerals of milk. Reproduction Nutrition Development 45: 473-483.
- Gilbert, C.L., Goode, J.A. and McGrath, T.J., 1994. Pulsatile secretion of oxytocin during parturition in the pig: temporal relationship with fetal expulsion. Journal of Physiology 475: 129-137.
- Goransson, L., 1990. The effect on late pregnancy feed allowance on the composition of the sow's colostrum and milk. Acta Veterinaria Scandinavica 31: 109-115.
- Gueguen, L. and Salmon-Legageur, E., 1959. La composition du lait de truie: variations des teneurs en quelques elements mineraux (P, Ca, K, Na, Mg). Comptes rendus hebdomadaires des séances de l'Académie des sciences 249: 784-786.
- Gurr, M.I., 1981. Review of the progress in dairy science: human and artificial milks for infant feeding. Journal of Dairy Research 48: 519-554.

- Harmon, B.G., Liu, C.T., Cornelius, S.G., Pettigrew, J.E., Baker, D.H. and Jensen, A.H., 1974. Efficacy of different phosphorus supplements for sows during gestation and lactation. Journal of Animal Science 39: 1117-1122.
- Hartmann, P.E., 1973. Changes in the composition and yield of the mammary secretions of cows during the initation of lactation. Journal of Endocrinology 59: 231-247.
- Hartmann, P.E. and Holmes, M.A., 1989. Sow lactation. In: Barnett, J.L. and Hennessy, D.P. (eds.) Manipulating pig production II. Australasian Pig Science Association, Werribee, Victoria, Australia, pp. 72-97.
- Heidebrecht, A.A., MacVicar, R., Ross, O.R. and Whitehair, C.K., 1951. Composition of swine milk. I. Major constituents and carotene, vitamin A and vitamin C. Journal of Nutrition 44: 43-50.
- Heying, E.K., Grahn, M., Pixley, K.V., Rocheford, T. and Tanumihardjo, S.A., 2013. High-provitamin A carotenoid (orange) maize increases hepatic vitamin A reserves of offspring in a vitamin A-depleted sow-piglet model during lactation. Journal of Nutrition 143: 1141-1146.
- Hidiroglou, M. and Batra, T.R., 1995. Concentrations of vitamin C in milk of sows and plasma of piglets. Canadian Journal of Animal Science 75: 275-277.
- Holmes, M.A. and Hartmann, P.E., 1993. Concentration of citrate in the mammary secretion of sows during lactogenesis II and established lactation. Journal of Dairy Research 60: 319-326.
- Hurley, W.L. and Bryson, J.M., 1999. Enhancing sow productivity through an understanding of mammary gland biology and lactation physiology. Pig News and Information 20: 125N-130N.
- Hurley, W.L. and Grieve, R.C.J., 1988. Total and differential cell counts and N-acetyl-β-D-glucosaminidase activity in sow milk during lactation. Veterinary Research Communications 12: 149-153.
- Hurley, W.L. and Theil, P.K., 2013. Immunoglobulins in mammary secretions. In: McSweeney, P.L.H. and Fox, P.F. (eds.) Advanced dairy chemistry, volume 1A: proteins: basic aspects (4th Edition). Springer Science, New York, NY, USA, pp. 275-294.
- Jackson, J.R., 1990. Effect of gestation length and supplemental dietary fat on colostrum and milk composition in swine. PhD Thesis, University of Illinois, Urbana-Champaign, IL, U.S.A., pp. 1-129.
- Jackson, J.R., Hurley, W.L., Easter, R.A., Jensen, A.H. and Odle, J., 1995. Effects of induced or delayed parturition and supplemental dietary fat on colostrum and milk composition in sows. Journal of Animal Science 73: 1906-1913.
- Jaeger, L.A., Lamar, C.H., Bottoms, G.D. and Cline, T.R., 1987. Growth-stimulating substances in porcine milk. American Journal of Veterinary Research 48: 1531-1533.
- Jensen, P.T., 1978. Tryspin inhibitor in sow colostrum and its function. Annales De Recherches Veterinaires 9: 225-228.
- Jensen, P.T. and Pedersen, K.B., 1979. Studies on immunoglobulins and trypsin inhibitor in colostrum and milk from sows and in serum of their piglets. Acta Veterinaria Scandinavica 20: 60-72.
- Kandeh, M.M., Park, Y.W., Pond, W.G. and Young, L.D., 1993. Milk cholesterol concentration in sows selected for three generations for high or low serum cholesterol. Journal of Animal Science 71: 1100-1103.
- Keenan, T.W., King, J.L. and Colenbrander, V.F., 1970. Comparative analysis of mammary tissue and milk lipids of the sow. Journal of Animal Science 30: 806-811.

- Kensinger, R.S., Collier, R.J., Bazer, F.W., Ducsay, C.A. and Becker, H.N., 1982. Nucleic acid, metabolic and histological changes in gilt mammary tissue during pregnancy and lactogenesis. Journal of Animal Science 54: 1297-1308.
- Kent, J.C., Arthur, P.G. and Hartmann, P.E., 1998. Citrate, calcium, phosphate and magnesium in sows' milk at initiation of lactation. Journal of Dairy Research 65: 55-68.
- Kim, Y.Y. and Mahan, D.C., 2001. Prolonged feeding of high dietary levels of organic and inorganic selenium to gilts from 25 kg body weight through on parity. Journal of Animal Science 79: 956-966.
- King, R.H., 1998. Dietary amino acids and milk production. In: Verstegen, M.W.A., Moughan, P.J. and Schrama, J.W. (eds.) The lactating sow. Wageningen Pers, Wageningen, The Netherlands, pp. 131-141.
- King, R.H., Toner, M.S., Dove, H., Atwood, C.S. and Brown, W.G., 1993. The response of first-litter sows to dietary protein level during lactation. Journal of Animal Science 71: 2457-2463.
- Klaver, J., Van Kempen, G.J.M., De Lange, P.G.B., Verstegen, M.W.A. and Boer, H., 1981. Milk composition and daily yield of different milk components as affected by sow condition and lactation/feeding regimen. Journal of Animal Science 52: 1091-1097.
- Klobasa, F. and Butler, J.E., 1987. Absolute and relative concentrations of immunoglobulins G, M, and A, and albumin in lacteal secretion of sows of different lactation numbers. American Journal of Veterinary Research 48: 176-182.
- Klobasa, F., Werhahn, E. and Butler, J.E., 1987. Composition of sow milk during lactation. Journal of Animal Science 64: 1458-1466.
- Konar, A., Thomas, P.C. and Rook, J.A.F., 1971. The concentrations of some water-soluble constituents in the milks of cows, sows, ewes and goats. Journal of Dairy Research 38: 333-341.
- Krakowski, L., Krzyzanowski, J., Wrona, Z., Kostro, K., and Siwicki, A.K., 2002. The influence of nonspecific immunostimulation of pregnant sows on the immunological value of colostrum. Veterinary Immunology and Immunopathology 87: 89-95.
- Krogh, U., Flummer, C., Jensen, S.K. and Theil, P.K., 2012. Colostrum and milk production of sows is affected by dietary conjugated linoleic acid. Journal of Animal Science 90: 366-368.
- Kusina, J., Pettigrew, J.E., Sower, A.F., White, M.E., Crooker, B.A. and Hathaway, M.R., 1999. Effect of protein intake during gestation and lactation on the lactational performance of primiparous sows. Journal of Animal Science 77: 931-941.
- Lauridsen, C. and Danielsen, V., 2004. Lactational dietary fat levels and sources influence milk composition and performance of sows and their progeny. Livestock Production Science 91: 95-105.
- Lauridsen, C., Engel, H., Jensen, S.K., Craig, A.M. and Traber, M.G., 2002. Lactating sows and suckling piglets preferentially incorporate *RRR* over all-*rac*-α-tocopheryl into milk, plasma tissues. Journal of Nutrition 132: 1258-1264.
- Lauridsen, C. and Jensen, S.K., 2005. Influence of supplementation of all-*rac*-α-tocopheryl acetate preweaning and vitamin C postweaning on α-tocopherol and immune responses of piglets. Journal of Animal Science 83: 1274-1286.
- Laws, J., Amusquivar, E., Laws, A., Herrera, E., Lean, L.J., Dodds, P.F. and Clarke, L., 2009. Supplementation of sows diets with oil during gestation: sow body condition, milk yield and milk composition. Livestock Science 123: 88-96.
- Le Dividich, J., Rooke, J.A. and Herpin, P., 2005. Nutrition and immunological importance of colostrum for the new-born pig. Journal of Agricultural Science 143: 469-485.

- Le Huërou-Luron, I. and Ferret-Bernard, S., 2015. Development of gut and gut-associated lymphoid tissues in piglets. Role of maternal environment. Chapter 15. In: Farmer, C. (ed.) The gestating and lactating sow. Wageningen Academic Publishers, Wageningen, the Netherlands, pp. 335-355.
- Le Jan, C., 1995. Epithelial cells in sow mammary secretions. Advances in Experimental Medicine and Biology 371A: 233-234.
- Lee, C.S. McCauley, I.M. and Hartmann, P.E., 1983. Light and electron microscopy of cells in pig colostrum, milk and involution secretion. Acta Anatomica 116: 126-135.
- Leonard, S.G., Sweeney, T., Babar, B., Lynch, B.P. and O'Doherty, J.V., 2010. Effect of maternal fish oil and seaweed extract supplementation on colostrum and milk composition, humoral immune response, and performance of suckled piglets. Journal of Animal Science 88: 2988-2997.
- Loisel, F., Farmer, C., Ramackers, P. and Quesnel, H., 2013. Effects of high fiber intake during late pregnancy on sow physiology, colostrum production, and piglet performance. Journal of Animal Science 91: 5269-5279.
- Loudenslager, M.J., Ku, P.K., Whetter, P.A., Ullrey, D.E., Whitehair, C.K., Stowe, H.D. and Miller, E.R., 1986. Importance of diet of dam and colostrum to the biological antioxidant status and parenteral iron tolerance of the pig. Journal of Animal Science 63: 1905-1914.
- Lyberg, K., Andersson, H.K., Simonsson, A. and Lindberg, J.E., 2007. Influence of different phosphorus levels and phytase supplementation in gestation diets on sow performance. Journal of Animal Physiology and Animal Nutrition 91: 304-311.
- Maffeo, G., Damasio, M., Balabio, R. and Jochle, W., 1987. Detection of prostaglandin-like substances in sow's milk. Zuchthygiene 22: 209-214.
- Mahan, D.C., 1991. Assessment of the influence of dietary vitamin E on sows and offspring in three parities: reproductive performance, tissue tocopherol, and effects on progeny. Journal of Animal Science 69: 2904-2917.
- Mahan, D.C., 2000. Effect of organic and inorganic selenium sources and levels on sow colostrum and milk selenium content. Journal of Animal Science 78: 100-105.
- Mahan, D.C., Becker, D.E., Harmon, B.G. and Jensen, A.H., 1971. Effect of protein levels and *opaque-2* corn on sow milk composition. Journal of Animal Science 32: 482-496.
- Mahan, D.C., Kim, Y.Y and Stuart, R.L., 2000. Effect of vitamin E sources (RRR- or all-*rac*-α-tocopheryl acetate) and levels on sow reproductive performance, serum, tissue, and milk α-tocopherol contents over a five-parity period, and the effects on the progeny. Journal of Animal Science 78: 110-119.
- Mahan, D.C., Moxon, A.L. and Hubbard, M., 1977. Efficacy of inorganic selenium supplementation to sow diets on resulting carry-over to their progeny. Journal of Animal Science 45: 738-746.
- Mahan, D.C. and Newton, E.A., 1995. Effect of initial breeding weight on macro- and micromineral composition over a three-parity period using a high-producing sow genotype. Journal of Animal Science 73: 151-158.
- Mahan, D.C and Peters, J.C., 2004. Long-term effects of dietary organic and inorganic selenium sources and levels on reproducing sows and their progeny. Journal of Animal Science 82: 1343-1358.
- Malm, A., Pond, W.G., Walker, Jr., E.F., Homan, M., Aydin, A. and Kirtland, D., 1976. Effect of polyunsaturated fatty acids and vitamin E level of the sow gestation diet on reproductive performance and on level of alpha tocopherol in colostrum, milk and dam and progeny blood serum. Journal of Animal Science 42: 393-399.

- Markowska-Daniel, I. and Pomorska-Mol, M., 2010. Shifts in immunoglobulins levels in the porcine mammary secretions during whole lactation period. Bulletin of the Veterinary Institute in Pulway 54: 345-349.
- Mateo, C.D., Peters, D.N. and Stein, H.H., 2004. Nucleotides in sow colostrum and milk at different stages of lactation. Journal of Animal Science 82: 1339-1342.
- Matte, J.J. and Girard, C.L., 1989. Effects of intramuscular injections of folic acid during lactation on folates in serum and milk and performance of sows and piglets. Journal of Animal Science 67: 426-431.
- Miller, G.M., Conrad, J.H. and Harrington, R.B., 1971. Effect of dietary unsaturated fatty acids and stage of lactation on milk composition and adipose tissue in swine. Journal of Animal Science 32: 79-83.
- Miller, M.B., Hartsock, T.G., Erez, B., Douglass, L. and Alston-Mills, B., 1994. Effect of dietary calcium concentrations during gestation and lactation in the sow on milk composition and litter growth. Journal of Animal Science 72: 1315-1319.
- Monaco, M.H., Gronlund, D.E., Bleck, G.T., Hurley, W.L., Wheeler, M.B. and Donovan, S.M., 2005. Mammary specific transgenic over-expression of insulin-like growth factor-I (IGF-I) increases pig milk IGF-I and IGF binding proteins, with no effect on milk composition or yield. Transgenic Research 14: 761-773.
- Mostyn, A., Sebert, S., Litten, J.C., Perkins, K.S., Laws, J., Symonds, M.E. and Clarke, L., 2006. Influence of porcine genotype on the abundance of thyroid hormones and leptin in sow milk and its impact on growth, metabolism and expression of key adipose tissue genes in offspring. Journal of Endocrinology 190: 631-639.
- Motyl, T., Ploszaj, T., Wojtasik, A., Kukulska, W. and Podgurniak, M., 1995. Polyamines in cow's and sow's milk. Comparative Biochemistry and Biophysics 111B: 427-433.
- Mulloy, A.L. and Malven, P.V., 1979. Relationships between concentrations of porcine prolactin in blood serum and milk of lactating sows. Journal of Animal Science 48: 876-881
- Neuhaus, U., 1961. Die milchleistung der sau und die zusammensetzung und eigenschaften der sauenmilch. Zeitschrift für Tierzüchtung und Züchtungsbiologie 75: 160-191.
- Nguyen, T.V., Yuan, L., Azevedo, S.P., Jeong, K.I., Gonzalez, A.M. and Saif, L.J., 2007. Transfer of maternal cytokines to suckling piglets: *in vivo* and *in vitro* models with implications for immunomodulation of neonatal immunity. Veterinary Immunology and Immunopathology 117: 236-248.
- Noble, M.S., Rodriguez-Zas, S., Cook, J.B., Bleck, G.T., Hurley, W.L. and Wheeler, M.B., 2002. Lactational performance of first-parity transgenic gilts expressing bovine α -lactalbumin in their milks. Journal of Animal Science 80: 1090-1096.
- Noblet, J. and Etienne, M., 1986. Effect of energy level in lactating sows on yield and composition of milk and nutrient balance of piglets. Journal of Animal Science 63: 1888-1896.
- O'Connor, D.L., Picciano, M.F., Roos, M.A. and Easter, R.A., 1989. Iron and folate utilization in reproducing swine and their progeny. Journal of Nutrition 119: 1984-1991.
- Oftedal, O.T., 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. Symposium of the Zoological Society of London 51: 33-85.
- Oftedal, O.T. and Iversen, S.J., 1995. Comparative analysis of nonhuman milks. A. Phylogenetic variation in the gross composition of milks. In: Jensen, R.G. (ed.) Handbook of milk composition. Academic Press, Inc., San Diego, CA, USA, pp. 749-789.
- Osterlundh, I., Holst, H. and Magnusson, U., 1998. Hormonal and immunological changes in blood and mammary secretion in the sow at parturition. Theriogenology 50: 465-477.

- Paape, M.J. and Tucker, H.A., 1966. Somatic cell content variation in fraction-collected milk. Journal of Dairy Science 49: 265-267.
- Pakkanen, R. and Aalto, J., 1997. Growth factors and antimicrobial factors in bovine colostrum. International Dairy Journal 7: 285-297.
- Park, Y.W., 2011. Milks of other domesticated mammals (pigs, yaks, reindeer, etc). In: Fuquay, J.W., Fox. P.F. and McSweeney, P.L.H. (eds.) Encyclopedia of dairy sciences, volume 3 (2nd Edition). Academic Press, Inc., San Diego, CA, USA, pp. 530-537.
- Park, Y.W., Kandeh, M., Chin, K.B., Pond, W.G. and Young, L.D., 1994. Concentrations of inorganic elements in milk of sows selected for high and low cholesterol. Journal of Animal Science 72: 1399-1402.
- Peaker, M., 1983. Secretion of ions and water. In: Mepham, T.B. (ed.) Biochemistry of lactation. Elsevier Science Publishers, Amsterdam, the Netherlands, pp. 285-305.
- Peaker, M. and Linzell, J.L., 1975. Citrate in milk: a harbinger of lactogenesis. Nature 253: 464.
- Peng, Y., Ren, F., Yin, J.D., Fang, Q., Li, F.N. and Li, D.F., 2010. Transfer of conjugated linoleic acid from sows to their offspring and its impact on the fatty acid profiles of plasma, muscle, and subcutaneous fat in piglets. Journal of Animal Science 88: 1741-1751.
- Perrin, D.R., 1955. The chemical composition of the colostrum and milk of the sow. Journal of Dairy Research 22: 103-107.
- Perrin, D.R., 1958. The calorific value of milk of different species. Journal of Dairy Research 25: 215-220.
- Peters, J.C. and Mahan, D.C., 2008. Effects of dietary organic and inorganic trace mineral levels on sow reproductive performances and daily mineral intakes over six parities. Journal of Animal Science 86: 2247-2260.
- Peters, J.C., Mahan, D.C., Wiseman, T.G. and Fastinger, N.D., 2010. Effect of dietary organic and inorganic micromineral source and level on sow body, liver, colostrum, mature milk, and progeny mineral compositions over six parities. Journal of Animal Science 88: 626-637.
- Pettigrew, Jr., J.E., 1981. Supplemental dietary fat for peripartal sows: a review. Journal of Animal Science 53: 107-117.
- Phipps, L.W. and Newbould, F.H.S., 1966. Determination of leucocyte concentrations in cow's milk with a Coulter counter. Journal of Dairy Research 33: 51-64.
- Pinelli-Saavedra, A., Calderon de la Barca, A.M., Hernandez, J., Valenzuela, R. and Scaife, J.R., 2008. Effect of supplementing sows' feed with α-tocopherol acetate and vitamin C on transfer of α-tocopherol to piglet tissues, colostrum, and milk: aspects of immune status of piglets. Research in Veterinary Science 85: 92-100.
- Pond, W.G. and Jones, J.R., 1964. Effect of level of zinc in high calcium diets on pigs from weaning through one reproductive cycle and on subsequent growth of their offspring. Journal of Animal Science 23: 1057-1060.
- Pond, W.G., Veum, T.L. and Lazar, V.A., 1965. Zinc and iron concentration of sows' milk. Journal of Animal Science 24: 668-670.
- Prunier, A., Messias de Bragança, M. and Le Dividich, J., 1997. Influence of high ambient temperature on performance of reproductive sows. Livestock Production Science 52: 123-133.
- Quesnel, H., 2011. Colostrum production by sows: variability of colostrum yield and immunoglobulin G concentrations. Animal 5: 1546-1553.
- Quesnel, H., Farmer, C. and Devillers, N., 2012. Colostrum intake: influence on piglet performance and factors of variation. Livestock Science 146: 105-114.

- Quesnel, H., Farmer, C. and Theil, P.K., 2015. Colostrum and milk production. Chapter 8. In: Farmer, C. (ed.) The gestating and lactating sow. Wageningen Academic Publishers, Wageningen, the Netherlands, pp. 173-192.
- Quesnel, H., Renaudin, A., Le Floc'h, N., Jondreville, C., Père, M.C., Taylor-Pickard, J.A. and Le Dividich, J., 2008. Effect of organic and inorganic selenium sources in sow diets on colostrum production and piglet response to a poor sanitary environment after weaning. Animal 2: 859-866.
- Renaudeau, D. and Noblet, J., 2001. Effects of exposure to high ambient temperature and dietary protein level on sow milk production and performance of piglets. Journal of Animal Science 79: 1540-1548.
- Reynolds, L. and Rook, J.A.F., 1977. Intravenous infusion of glucose and insulin in relation to milk secretion in the sow. British Journal of Nutrition 37: 45-52.
- Richert, B.T., Goodband, R.D., Tokach, M.D. and Nelssen, J.L., 1997. Increasing valine, isoleucine, and total branched-chain amino acids for lactating sows. Journal of Animal Science 75: 2117-2128.
- Rolinec, M., Biro, D., Stastny, P., Galik, B., Simko, M. and Juracek, M., 2012. Immunoglobulins in colostrum of sows with porcine reproductive and respiratory syndrome PPRS. Journal of Central European Agriculture 13: 303-311.
- Rooke, J.A., Bland, I.M. and Edwards, S.A., 1998. Effect of feeding tuna oil or soyabean oil as supplements to sows in late pregnancy on piglet tissue composition and viability. British Journal of Nutrition 80: 273-280.
- Salman, S., Khol-Parisini, A., Schafft, H., Lahrssen-Wiederholt, M., Hulan, H.W., Dinse, D. and Zentek, J., 2009. The role of dietary selenium in bovine mammary gland health and immune function. Animal Health Research Reviews 10: 21-34.
- Schieck, S.J., Kerr, B.J., Baidoo, S.K., Shurson, G.C. and Johnston, L.J., 2010. Use of crude glycerol, a biodiesel coproduct, in diets for lactating sows. Journal of Animal Science 88: 2648-2656.
- Schmid, A., Collomb, M., Bee, G., Butikofer, U., Wechsler, D., Eberhard, P. and Sieber, R., 2008. Effect of dietary alpine butter rich in conjugated linoleic acid on milk fat composition of lactating sows. British Journal of Nutrition 100: 54-60.
- Schoenherr, W.D., Staley, T.S. and Cromwell, G.L., 1989. The effects of dietary fat or fiber addition on yield and composition of milk from sows housed in a warm or hot environment. Journal of Animal Science 67: 482-495.
- Schollenberger, A., Degorski, A., Frymus, T and Schollenberger, A., 1986a. Cells of sow mammary secretions. I. Morphology and differential counts during lactation. Journal of Veterinary Medicine A 33: 31-38.
- Schollenberger, A., Degorski, A., Frymus, T and Schollenberger, A., 1986b. Cells of sow mammary secretions. II. Some properties of phagocytic cells. Journal of Veterinary Medicine A 33: 39-46.
- Schollenberger, A., Degorski, A., Frymus, T and Schollenberger, A., 1986c. Cells of sow mammary secretions. III. Characterization of lymphocyte populations. Journal of Veterinary Medicine A 33: 353-359.
- Schone, F., Leiterer, M., Hartung, H., Jahreis, G. and Tischendorf, F., 2001. Rapeseed glucosinolates and iodine in sows affect the milk iodine concentration and the iodine status of piglets. British Journal of Nutrition 85: 659-670.
- Schone, F., Leiterer, M., Jahreis, G. and Rudolph, B., 1997. Effect of rapeseed feedstuffs with different glucosinolate content and iodine administration on gestating and lactating sow. Journal of Veterinary Medicine A 44: 325-339.

- Seerley, R.W., Snyder, R.A. and McCampbell, H.C., 1981. The influence of sow dietary lipids and choline on piglet survival, milk and carcass composition. Journal of Animal Science 52: 542-550.
- Seynaeve, M., De Wilde, R., Janssens, G. and De Smet, B., 1996. The influence of dietary salt level on water consumption, farrowing, and reproductive performance of lactating sows. Journal of Animal Science 74: 1047-1055.
- Sheffy, B.E., Shahani, K.M., Grummer, R.H., Phillips, P.H. and Sommer, H.H., 1952. Nitrogen constituents of sow's milk as affected by ration and stage of lactation. Journal of Nutrition 48: 103-114.
- Shurson, G.C., Hogberg, M.G., DeFever, N., Radecki, S.V. and Miller, E.R., 1986. Effects of adding fat to the sow lactation diet on lactation and rebreeding performance. Journal of Animal Science 62: 672-680.
- Shurson, G.C. and Irvin, K.M., 1992. Effects of genetic line and supplemental dietary fat on lactation performance of Duroc and Landrace sows. Journal of Animal Science 70: 2942-2949.
- Simmen, F.A., Whang, K.Y., Simmen, R.C.M., Peterson, G.A., Bishop, M.D. and Irvin, K.M., 1990. Lactational variation and relationship to postnatal growth of insulin-like growth factor-I in mammary secretions from genetically diverse sows. Domestic Animal Endocrinology 7: 199-206.
- Staszkiewicz, J., Franczak, A., Kotwica, G. and Koziorowski, M., 2004. Secretion of estradiol-17β by porcine mammary gland of ovariectomized steroid-treated sows. Animal Reproduction Science 81: 87-95.
- Tan, T.J., Schober, D.A. and Simmen, F.A., 1990. Fibroblast mitogens in swine milk include an epidermal growth factor-related peptide. Regulatory Peptides 27: 61-74.
- Tao, N., Ochonicky, K.L., German, B., Donovan, S.M. and Lebrilla, C.B., 2010. Structural determination and daily variations of porcine milk oligosaccharides. Journal of Agricultural and Food Chemistry 58: 4653-4659.
- Taugbøl, O., Farmstad, T. and Saarem, K., 1993. Supplements of cod liver oil to lactating sows. Influence on milk fatty acid composition and growth performance of piglets. Journal of Veterinary Medicine A 40: 437-443.
- Theil, P.K., Jørgensen, H and Jakobsen, K., 2004. Energy and protein metabolism in lactating sows fed two levels of dietary fat. Livestock Production Science 89: 265-276.
- Theil, P.K., Lauridsen, C. and Quesnel, H., 2014. Neonatal piglet survival: impact of sow nutrition around parturition on foetal glycogen deposition, and production and composition of colostrum and transient milk. Animal 8: 1021-1030.
- Tilton, S.L., Miller, P.S., Lewis, A.J., Reese, D.E. and Ermer, P.M., 1999. Addition of fat to the diets of lactating sows: I. Effects on milk production and composition and carcass composition of the litter at weaning. Journal of Animal Science 77: 2491-2500.
- Van den Brand, H., Heetkamp, M.J.W., Soede, N.M., Schrama, J.W. and Kemp, B., 2000. Energy balance of lactating primiparous sows as affected by feeding level and dietary energy source. Journal of Animal Science 78: 1520-1528.
- Venn, J.A.J, McCance, R.A. and Widdowson, E.M., 1947. Iron metabolism in piglet anaemia. Journal of Comparative Pathology and Therapeutics 57: 314-325.
- Veum, T.T., Gallo, J.T., Pond, W.G., Van Vleck, L.D. and Loosli, J.K., 1965. Effect of ferrous fumarate in the lactation diet on sow milk iron, pig hemoglobin and weight gain. Journal of Animal Science 24: 1169-1173.

- Wang, S.P., Yin, Y.L., Qian, Y., Li, L.L., Li, F.N., Tan, B.E., Tang, X.S. and Huang, R.L., 2011. Effects of folic acid on the performance of suckling piglets and sows during lactation. Journal of the Science of Food and Agriculture 91: 2371-2377.
- Westrom, B.R., Ekman, R., Svendsen, L., Svendsen, J. and Karlsson, B.W., 1987. Levels of immunoreactive insulin, neurotensin, and bombesin in porcine colostrum and milk. Journal of Pediatric Gastroenterology and Nutrition 6: 460-465.
- White, C.E., Head, H.H., Bachman, K.C. and Bazer, F.W., 1984. Yield and composition of milk and weight gain of nursing pigs from sows fed diets containing fructose or dextrose. Journal of Animal Science 59: 141-150.
- Whittestone, W.G., 1952. The physical properties of sow's milk as a function of stage of lactation. Journal of Dairy Research 19: 330-334.
- Wu, G. and Knabe, D.A., 1994. Free and protein-bound amino acids in sow's colostrum and milk. Journal of Nutrition 124: 415-424.
- Wuryastuti, H., Stowe, H.D., Bull, R.W. and Miller, E.R., 1993. Effects of vitamin E and selenium on immune responses of peripheral blood, colostrum, and milk leukocytes of sows. Journal of Animal Science 71: 2464-2472.
- Yan, W., Wiley, A.A., Bathgate, A.D., Frankshun, A.L., Lasano, S., Crean, B.D., Steinetz, B.G., Bagnell, C.A. and Bartol, F.F., 2006. Expression of LGR7 and LGR8 by neonatal porcine uterine tissues and transmission of milk-borne relaxin into the neonatal circulation by suckling. Endocrinology 147: 4303-4310.
- Yao, W., Li, J., Wang, J.J., Zhou, W., Wang, Q., Zhu, R., Wang, F. and Thacker, P., 2012. Effects of dietary ratio of n-6 to n-3 polyunsaturated fatty acids on immunoglobulins, cytokines, fatty acid composition, and performance of lactating sows and suckling piglets. Journal of Animal Science and Biotechnology 3: 43-50.
- Yoon, I. and McMillan, E., 2006. Comparative effects of organic and inorganic selenium on selenium transfer from sows to nursing pigs. Journal of Animal Science 84: 1729-1733.
- Yvon, M., Levieux, D., Valluy, M.C., Pelissier, J.P. and Mirand, P.P., 1993. Colostrum protein digestion in newborn lambs. Journal of Nutrition 123: 586-596.
- Zhan, X., Qie, Y., Wang, M., Li, X. and Zhao, R., 2011. Selenomethionine: an effective selenium source for sow to improve Se distribution, antioxidant status, and growth performance of pig offspring. Biological Trace Element Research 142: 481-491.
- Zou, S., McLaren, D.G. and Hurley, W.L., 1992. Pig colostrum and milk composition: comparisons between Chinese Meishan and US breeds. Livestock Production Science 30: 115-127.