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Comparison of the nutritional value and fatty acid composition of milk from four South American camelid species

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Abstract: The nutritional value, whey protein, and the fatty acid (FA) composition of milk from four South American camelids (SAC) (vicuna, *Vicugna vicugna* (Molina, 1782); alpaca, *Vicugna pacos* (Linnaeus, 1758); guanaco, *Lama guanicoe* (Müller, 1776); llama, *Lama glama* (Linnaeus, 1758)) were evaluated and compared with milk from old-world camelids. Samples were collected from healthy animals from the northwest (llama, alpaca, and vicuna) and Patagonia (guanaco) areas of Argentina. Gross composition of milk from SAC showed a higher protein, lactose, and lipid content than camel milk. Serum albumin and α-lactalbumin were the dominant whey proteins, followed by immunoglobulin G (IgG). The FA profile showed from 4:0 to 24:0 FA, with a high level of conjugated fatty acid (CLA; 1.05–1.64 g/100 g of FAME) and its precursor, vaccenic acid. Desaturase activity of C16 and CLA was quite similar between species but was significantly different for C14. Camelid milk showed a lower atherogenicity index than ruminant milk. This is the first time that a comparative study involving four species of SAC was carried out to contribute to the general knowledge of the physiology of new-world camelids. Their milk was determined to be of high nutritional quality, allowing it to be considered an alternative food item for humans in the semi-arid region of South America.

Key words: vicuna, *Vicugna vicugna*, guanaco, *Lama guanicoe*, llama, *Lama glama*, alpaca, *Vicugna pacos*, milk composition, fatty acids.

Résumé : La valeur nutritive et la composition des protéines du lactosérum et des acides gras (AG) du lait des quatre camélidés sud-américains (CSA) (la vigogne, *Vicugna vicugna* (Molina, 1782); l'alpaga, *Vicugna pacos* (Linnaeus, 1758); le guanaco, *Lama guanicoe* (Müller, 1776); le lama, *Lama glama* (Linnaeus, 1758)) ont été évaluées et comparées à celles de camélidés de l'ancien monde. Des échantillons ont été prélevés d'animaux sains des régions argentines du nord-ouest (lama, alpaga et vigogne) et de la Patagonie (guanaco). La composition brute du lait des CSA présente de plus fortes teneurs en protéines, en lactose et en lipide que le lait de chameau. L'albumine et l'α-lactalbumine sont les protéines dominantes du lactosérum, suivies de l'immunoglobuline G (IgG). Le profil d'AG contient des AG allant de 4 : 0 à 24 : 0, avec une forte proportion d'acide gras conjugué (ALC; 1,05–1,64 g/100 g EMAG) et son précurseur, l'acide vaccénique. L'activité de la désaturase pour l'acide gras C16 et l'ALC est très semblable d'une espèce à l'autre, mais significativement différente en ce qui concerne le C14. Le lait de camélidés présente un indice d'athérogénicité plus faible que le lait de ruminants. Cette première étude comparative portant sur les quatre espèces de CSA contribue à accroître les connaissances générales sur la physiologie des camélidés du nouveau monde. Il est ainsi établi que leur lait est de haute qualité nutritive, de sorte qu'il pourrait constituer un aliment prometteur pour les humains dans les régions semi-arides de l'Amérique du Sud. [Traduit par la Rédaction]

Mots-clés : vigogne, *Vicugna vicugna*, guanaco, *Lama guanicoe*, lama, *Lama glama*, alpaga, *Vicugna pacos*, composition du lait, acides gras.

Introduction

Camelids are classified within the order Artiodactyla, suborder Tylopoda, and family Camelidae; they include the old-world and the new-world camelids, which are subdivided at the tribe level into Lamini and Camelini, respectively (Wheeler 2012). Within the first group, the genus *Camelus* Linnaeus, 1758 is represented by the one-humped camel (*Camelus dromedarius* Linnaeus, 1758; also known as dromedary) and the two-humped camel (*Camelus bactrianus* Linnaeus, 1758; also known as Bactrian camel). Within the second group, known as the South American camelids (SAC), are the genera *Lama* G. Cuvier, 1800 and *Vicugna* Lesson, 1842. *Lama* and *Vicugna* genera evolved in South America approximately 2 million years ago (Harrison 1985; Stanley et al. 1994) and currently in-

cludes two domesticated species (alpaca, *Vicugna pacos* (Linnaeus, 1758); llama, *Lama glama* (Linnaeus, 1758)) and their two wild ancestors (vicuna, *Vicugna vicugna* (Molina, 1782); guanaco, *Lama guanicoe* (Müller, 1776)). All four species are culturally and commercially important for meat, fiber production, dung, and service as pack animals in South America (Wheeler 2012).

Currently, the distribution of SAC is restricted to the semi-arid regions, ranging from sea level to the Andean mountains (5000 m above sea level) of Bolivia, Perú, Argentina, and Chile (Quispe et al. 2009). In all of these areas, climate conditions are extreme; therefore, SAC has several survival adaptations like its characteristic fiber.

The llama is the most popular species reared in South America as a pack animal and for meat consumption. In northwestern

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Argentina, llama meat is typically used in sausages and speciality dishes. Consequently, the nutritional value of llama meat has been well established over the years (Coates and Ayerza 2004; Polidori et al. 2007). On the other hand, alpaca is almost exclusively held for fiber production and therefore it has been exported to other countries. Incas domesticated both llama and alpaca approximately 5000–6000 years ago (Wheeler 2012). Guanaco has adapted to a wide range of environments from the Patagonia regions of Chile and Argentina up to the Andean region of Perú. The smallest species, vicuna, is currently classified as endangered and protected by legislation in Perú, Bolivia, Argentina, and Chile. As such, some farmers raise vicuna for commercial purposes because of its finest fiber, along with goat (*Capra hircus* Linnaeus, 1758) or sheep (*Ovis aries* Linnaeus, 1758).

It is well known that milk composition varies during lactation and among species (Oftedal 1984), depending on factors such as feeding, breeding age, and time of the year (Palmquist 2006). The lactation period of SAC is around 8 months, with newborns dependent on maternal milk. Knowing the composition of milk enables one to supplement the feed of nursing camelids (crias); it also provides a better understanding of the nutrient requirements of the dam.

Although camelid rearing has increased over the years, the milk is still mainly destined to feed the offspring and is consumed only by people of the region. Milk and dairy products from *Camelus* are usually consumed in countries such as Pakistan, Somalia, and Ethiopia. Composition of milk from old-world camels has been extensively investigated (Mohamed et al. 2005; El-Agamy et al. 2009; Zhao et al. 2015). To the best of our knowledge, few studies have described the composition of milk from SAC; those studies mostly examined milk from llamas (Fernández and Oliver 1988; Riek and Gerken 2006; Schoos et al. 2008) and to a lesser extent alpacas (Parraguez et al. 2003; Martini et al. 2015). Research on the composition of milk from wild species are still scarce (for vicuna; Fernández et al. 1997; Medina et al. 2004) or inexistent (for guanaco).

Milk fatty acid (FA) composition is very complex, with FA consisting of 4 to 26 carbons. The milk FA profile of a species is the result of (*i*) direct uptake of circulating FA, (*ii*) de novo synthesis of FA by the mammary gland, and (*iii*) further modification of FA in the mammary gland by enzymes (elongation and desaturation process) (Iverson and Oftedal 1995). Whereas FA synthesis in the liver and adipose tissue produces primarily palmitate (16:0), the mammary gland synthesizes large amounts of medium-chain FA (8:0–12:0) by FA synthase.

The length of the de novo synthesized FA depends on the properties of enzymes involved in the synthesis pathway. FA synthase acts in the elongation process; in the mammary gland, the synthesis is terminated by thioesterase before the 16-carbon length is reached. Depending on the properties of thioesterase, this pathway may be affected after elongation to 8–14 carbons (Neville et al. 1983). Desaturase enzymes also act in the mammary gland on medium- and long-chain FA to produce the corresponding monounsaturated fatty acids (MUFA).

Milk from ruminants mainly differ in the quantity of medium-chain FA; the level of 14:0 FA is very constant, near 10% (Iverson and Oftedal 1995). Differences in medium-chain FA among Artiodactyla have been extensively reported (Osthoff et al. 2009, 2012, 2017).

There are no comparative studies regarding the gross composition and FA profile of milk from the four SAC species, old-world camels, and ruminants.

Since the genera *Lama* and *Vicuna* have evolved in different regions of South America, implying adaptations to the different environmental conditions where they are found, variations in the composition of their milk could occur. Furthermore, human domestication after so many years could have influenced milk composition. Therefore, the aim of the present study was to evaluate the milk chemical composition, whey proteins (WP), and FA profile of the four SAC species. Additionally, we compared the composition of milk from SAC with the composition of milk from the old-world camelid genus *Camelus* as the closest relative group and from other Artiodactyla (ruminants) to improve our knowledge of closely related mammals.

Materials and methods

Milk samples

Over a month, milk samples from vicuna (*n* = 10), llama (*n* = 12), and alpaca (*n* = 7) were obtained weekly from farms located in northwestern Argentina (Andean region known as Puna), whereas milk samples from guanaco (*n* = 6) were obtained from southern Argentina (Patagonia region) during the same period. The milk samples were collected in autumn (April–May) from healthy adult females (from 3 to 8 years of age) of varying lactation times (from 30 up to 98 days) (Table 1). Mammary glands were visually examined and palpated for lesions or abnormal consistency. Milk samples were collected in the morning by hand milking, with the first few millilitres (3–5 mL) being discarded and the rest being collected in a sterile flask. No milk-letting agent was used in this study. Samples were delivered by refrigerated transport (4 °C) to the laboratory and kept at –20 °C until further analysis.

Chemical analysis

Milk samples were analyzed for proteins and fat using the ultrasound method (EKO-MILK analyser, Milkana Kam 98-2A), which was calibrated against the Kjeldahl and Folch standards, respectively, using one milk sample each from guanaco, alpaca, llama, and vicuna. Lactose was determined using the UV lactose–galactose method (Boehringer Mannheim, Mannheim, Germany). Total solids (TS) were analyzed according to IDF–FIL (1982). WP, obtained after acid precipitation of caseins, was measured according to Bradford (1976) and additional casein was estimated by subtracting WP from the total protein. Ash was calculated by subtracting total protein (i.e., WP + casein), lactose, and lipid content from TS. pH was measured by a Metrohm peachimeter (model 692; Metrohm AG, Herisau, Switzerland). Gross energy was calculated using Perrin's (1958) formula: GE (MJ/100 g) = 39.8(fat%) + 23.9(protein%) + 16.7(lactose%).

Milk WP electrophoresis

A portion of each milk sample (10 mL) was centrifuged at 6000 r/min for 20 min at 4 °C and fat was carefully removed. Precipitation of caseins was performed by adding a few millilitres of 10% (*v*/*v*) acetic acid until a pH of 4.5 was reached, followed by centrifugation at 7500 r/min for 20 min at 4 °C. The supernatant was collected for further analysis. An electrophoretic analysis with a 10% SDS–PAGE gel was performed following the methodology outlined in Harris and Angal (1989) and protein bands were observed after staining with Coomassie Brilliant Blue R-250 (0.1%) for 12 h. Milk WP of goat colostrum was used as reference standard.

Lipid analysis

Total lipids were extracted using a chloroform–methanol mixture (2:1, *v*/*v*) according to Folch et al. (1957). Fatty acid methyl esters (FAME) analyses were performed according to Taboada et al. (2015).

One microlitre of FAME, dissolved in hexane, was injected into a gas chromatograph (model 6890N; Agilent Technologies, Santa Clara, California, USA) equipped with a flame ionization detector and an automatic injector (model 7683; USA) connected to an HP-88 capillary column (100 m × 0.25 mm × 0.20 μm; Agilent Technologies). Gas chromatograph conditions were as follows: injector temperature was 255 °C; the initial oven temperature of 75 °C was increased to 165 °C at 8 °C/min and held there for 35 min, increased to 210 °C at 5.5 °C/min and held for 2 min, and then increased to 240 °C at 15 °C/min and held for 3 min. Detector temperature was 280 °C. Nitrogen was used as the carrier gas at a

Table 1. Gross composition of milk from four South American camelids (alpaca, *Vicugna pacos*; llama, *Lama glama*; guanaco, *Lama guanicoe*; vicuna, *Vicugna vicugna*), and comparison of data from the South American camelids, two old-world camel species (Bactrian camel, *Camelus bactrianus*; dromedary, *Camelus dromedarius*), and ruminants (goat, *Capra hircus*; cow, *Bos taurus*; sheep, *Ovis aries*; giraffe, *Giraffa camelopardalis*).

| | South American camelids | | | | South American camelids | | | Asian camels (old-world) | | Ruminants | | | |
| | Domestic species | | Wild species | | | | | | | | | | |
Component (g/100 g of milk)	Alpaca (n = 7)	Llama (n = 12)	Guanaco (n = 6)	Vicuna (n = 10)	Alpaca*	Llama†	Vicuna‡	Bactrian§	Dromedary§	Goat§	Cow§	Sheep§	Giraffe‖
Lactation (days)	30–69	31–98	34–79	33–88									
Total solids	15.15±0.87a	15.36±0.83a	16.63±0.32b	16.95±0.46b	15.06	15.6–16.3	NA	15.19	12.41	12.1	12.3	17.1	NA
Total protein	5.56±0.49b	4.58±0.36a	5.00±0.31ab	4.30±0.34a	4.5–5.6	4.2–4.3	3.7	4.09	3.96	3.0	3.2	5.3	4.9
Whey protein	0.88±0.03c	0.91±0.06c	0.53±0.06a	0.65±0.07b	NA	NA	0.5	1.02	0.93	0.7	0.7	1.2	1.8
Casein	4.68±0.48b	3.67±0.41a	4.47±0.26ab	3.65±0.27a	4.09	NA	3.2	3.01	2.4	2.3	2.5	4.1	3.1
Lactose	5.08±0.36a	5.17±0.50a	5.44±0.20a	7.05±0.28b	6.00	5.9–6.3	7.4	4.95	4.56	4.5	4.8	4.7	4.2
Lipid	3.80±0.28a	4.82±0.17b	5.50±0.56b	4.76±0.26ab	3.3–3.7	4.6–4.7	4.5	5.32	3.96	4.1	4.1	7.0	7.9
Ash	0.71±0.03a	0.79±0.04ab	0.70±0.04a	0.84±0.06b	0.67	0.88	NA	0.81	0.79	0.7	0.8	0.9	NA
pH	6.73±0.02a	6.76±0.01a	6.77±0.01a	6.75±0.01a	NA	6.8	7.02	6.55	NA	6.7	6.7	6.8	NA
Gross energy (MJ/100 g of milk)	368.9±22.8a	387.4±18.2ab	429.2±16.3c	410.0±16.4bc									

Note: *n* is the number of individual milk samples. NA is not available. Samples were analyzed in duplicate and results are expressed as mean ± SD. Different letters denote significant differences based on Tukey's honestly significant difference (HSD) test (P < 0.05).

*Chad et al. 2014; Martini et al. 2015.
†Schoos et al. 2008.
‡Fernández et al. 1997.
§Barlowska et al. 2011; El-Agamy 2006.
‖Osthoff et al. 2017.

flow rate of 18 mL/min at 38 psi. FA were identified by comparison of retention times with the methylated standards (Sigma, St. Louis, Missouri, USA). Conjugated fatty acid (CLA) and other FA were identified by comparison with the methyl ester standards (99%; Sigma–Aldrich). Results were expressed as percentage of the total FA determined.

Desaturase activities (for C14 and C16) were calculated using the product to substrate ratio (14:1/14:0 and 16:1/16:0) and the CLA to vaccenic ratio (CLA/vaccenic).

The atherogenicity index (AI) was estimated using the formula from Chilliard et al. (2003): AI = C12:0 + 4 × C14:0 + C16:0 / ΣUFA, where UFA is unsaturated fatty acids.

All solvents and reagents used were high performance liquid chromatography (HPLC) grade.

Statistical analysis

All milk samples were measured in duplicate and results were expressed as mean ± SD. All dependent variables measured from SAC milk (i.e., from chemical analysis, WP, and FA) were subjected to a one-way ANOVA, type III error, at $\alpha = 0.05$ to determine if there were significant differences in milk composition among SAC species. After the one-way ANOVA, a Tukey's honestly significant difference (HSD) test ($\alpha = 0.05$) was performed to compare mean values. All statistical analyses were conducted in Minitab® release 14 (Minitab Inc., State College, Pennsylvania, USA).

Results

Gross composition of milk

The proximate composition of milk obtained from alpaca, llama, guanaco, and vicuna is provided in Table 1, where it was compared with data from the literature for old-world camelids (Bactrian camel and dromedary). TS content was higher in milk from wild species (16–17 g/100 g of milk); TS content was significantly higher in milk from vicuna than milk from llama and alpaca. Total protein content ranged from 4.4 to 5.7 g/100 g of milk, with milk from alpaca having the highest content (Table 1). Casein was the most abundant protein in all SAC species, ranging from 3.7 to 4.8 g/100 g of milk. The highest casein content was in milk from alpaca, which was significantly different from the levels found in milk from llama and vicuna. Furthermore, casein content in milk from guanaco differed significantly from that of vicuna (Table 1). Regarding WP, a significantly lower content was observed in milk from wild species (~0.6 g/100 g of milk) compared with milk from domestic species (0.9 g/100 g of milk) (Table 1). Milk from vicuna had the highest and most significant level of lactose (7.06 g/100 g of milk) compared with the other three SAC species (averaged 5.2–5.4 g/100 g of milk). The lipid content in milk from llama and vicuna was ~4.8 g/100 g of milk, whereas the lipid content was the lowest (3.9 g/100 g of milk) in milk from alpaca and the highest in milk from guanaco (5.5 g/100 g of milk). The ash value varied from 0.7 to 0.8 g/100 g of milk. In general, llama and vicuna showed more similar protein, lipid, and ash contents compared with the other species. A similar pH value of ~6.7 was determined across the milk samples from the four species.

The gross energy value was significantly higher in milk from wild species (420–430 MJ/100 g of milk for vicuna and guanaco) than milk from domestic species (380 MJ/100 g of milk for alpaca and llama).

Milk WP

The electrophoretic gel (10% SDS–PAGE) of WP from milk of SAC is shown in Fig. 1, with goat colostrum as the reference standard for milk from a ruminant. Milk from SAC showed quite a similar pattern of bands as that of goat colostrum. The band that corresponded with immunoglobulin G subclass 1 (IgG$_1$) was present in both goat colostrum and milk from SAC (molecular mass ~150 kDa), whereas two bands of molecular mass ~86 kDa were

Fig. 1. The electrophoresis gel (10% SDS–PAGE) of milk whey proteins from (1) goat (*Capra hircus*) colostrum, (2) llama (*Lama glama*) milk, (3) vicuna (*Vicugna vicugna*) milk, (4) guanaco (*Lama guanicoe*) milk, and (5) alpaca (*Vicugna pacos*) milk. IgG$_1$, immunoglobulin G subclass 1; IgG$_H$, heavy-chain immunoglobulin G; α-La, α-lactalbumin. Color version online.
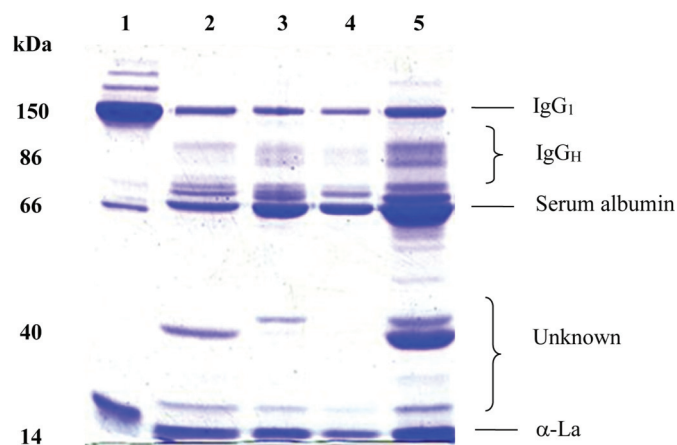
only observed in SAC. These two proteins probably correspond with the heavy chain of IgG (IgG$_H$).

Serum albumin (~66 kDa) and α-lactalbumin (~14 kDa) were the dominant WPs in camelids. Other unknown proteins, whose molecular masses were estimated around 18–40 kDa, were visualized in the milk from SAC but were not detected in goat colostrum.

FA profile

The FA profile of milk from the four species is given in Table 2. Saturated fatty acids (SFA) was the predominant FA in milk of camelids, ranging from 52 to 55 g/100 g of FAME. In all species, small amounts of short-chain FA (4:0–6:0) were found, with llama having the lowest level among the four species. Within SFAs, palmitic acid (16:0) was the most abundant (>25 g/100 g of FAME), followed by stearic acid (18:0; >10 g/100 g of FAME) and myristic acid (14:0; >10 g/100 g of FAME). Significantly higher level of pentanoic acid (15:0) was found in the milk from wild species (~0.12 g/100 g of FAME) than in the milk from domestic species (0.9–1.6 g/100 g of FAME) (Table 2).

The milk from camelids also had high levels of unsaturated fatty acids (UFA), ranging from 42 to 48 g/100 g of FAME, with oleic acid (18:1 *cis*-9) being the predominant UFA. We also detected a high level of vaccenic acid (18:1 *trans*-11), with a mean value of 2–3 g/100 g of FAME. We found significant differences ($P < 0.05$) in total polyunsaturated fatty acids (PUFA), with the lowest value in milk from llama (4.9 g/100 g of FAME) and the highest value in milk from guanaco (8.4 g/100 g of FAME) (Table 2). Among PUFA, we found high levels of linolenic acid (18:3 *n*–3) and conjugated linoleic acid (18:2 *cis*-9, *trans*-11; CLA) in milk from camelids.

Despite the differences mentioned above, the SFA/UFA ratio (1.1–1.3) and the atherogenicity index (1.4–1.7) were similar across all species. Desaturase activity in the mammary gland of the camelids, indirectly estimated by the product to substrate ratio, showed no statistical differences for the 16:1/16:0 and CLA/vaccenic desaturase indices. However, interspecific differences were determined for the 14:1/14:0 desaturase index (Table 2).

Discussion

Our results regarding the gross composition of milk from SAC are in agreement with those established for alpaca (Chad et al. 2014; Martini et al. 2015) and llama (Riek and Gerken 2006; Schoos et al. 2008) (Table 1). The chemical composition of milk from vi-

cuna that we determined, including the high level of lactose, is coincident with data reported for this species (Fernández et al. 1997; Riek and Gerken 2006) (Table 1). A high level of lactose (6 g/100 g of milk) was also found in milk from alpaca and llama (Jenness 1974; Chad et al. 2014). Compared with data from the literature, milk from old-world camels presented lower lactose levels than SAC, which were more similar to other Artiodactyla (El-Agamy 2006). Studies on milk from guanaco are almost nonexistent. In the present study, milk from guanaco had similar protein and lactose levels to milk from llama. Even though milk from guanaco had the highest fat content compared with the other species, it was not significantly different. Lipid content varies according to species and diet; however, the variation in fat content that we observed could not be associated with differences in vegetation between northwestern Argentina, where the other camelid species live, and southern Argentina. Because fat provides the greatest energy value, milk from guanaco has the highest energetic value between evaluated species.

WP and casein differ somewhat between the four SAC. WP to casein ratios of 1:4 were reported for llama, 1:5.3 for alpaca, 1:5.6 for vicuna, and 1:8.4 for guanaco; all values were within the range reported for ruminants (Oftedal 1984; Park 2006; Osthoff et al. 2017).

Comparing our results with data available for old-world camels, domesticated SAC showed similar TS, protein, fat, and ash levels to that of the Bactrian camel (Oftedal and Iverson 1995).

TS in milk from ruminants is around 12–17 g/100 g of milk, whereas TS in milk from camelids is near 15–17 g/100 g of milk. Within Artiodactyla, it has been previously reported that milk from camel and giraffe (*Giraffa camelopardalis* (Linnaeus, 1758)) have lower TS content compared with milk from other species (Oftedal and Iverson 1995); this is perhaps an adaptation to hot climates and the implication that more water is required by the young.

The nutritional composition of milk from alpaca, llama, vicuna, and guanaco did not differ much from that of other Artiodactyla (Table 1). Although lipid content in milk from the four SAC is within the range reported for milk from ruminants, protein content in milk from the four SAC is similar to that reported for milk from sheep and giraffe (5.7% and 4.9%, respectively) and higher than that reported for milk from goat and cow (*Bos taurus* Linnaeus, 1758) (~3.3%). Milk from SAC seems to have a higher lactose content than milk from old-world camels and ruminants.

The presence of three different subclasses of IgG in camelids (i.e., the conventional IgG$_1$ with heavy and light chains, and IgG$_2$ and IgG$_3$, which are known as heavy antibodies) was previously demonstrated (Hamers-Casterman et al. 1993). These subclasses of IgG were previously reported in milk from dromedary, as well as in sera from guanaco, llama, and alpaca (De Simone et al. 2006), which are in agreement with the pattern of band proteins shown in Fig. 1.

The prevalence of serum albumin and α-lactalbumin among WP agree with data reported for milk from old-world camels (El-Agamy et al. 2009; Zhao et al. 2015). In bovine milk, β-lactoglobulin is the most abundant WP (>50%), followed by α-lactalbumin (~26%); in camel milk, β-lactoglobulin is deficient (Zhao et al. 2015). β-Lactoglobulin was lacking in the four SAC.

We found unknown proteins with molecular masses 18–40 kDa. A previous study on Chinese Bactrian camel also found two unidentified bands with molecular masses 42–50 kDa (Zhao et al. 2015). According to Fernández and Oliver (1988), three peptone–protease bands are present in milk from llama; however, this was not confirmed. According to El-Agamy et al. (2009), casein and WP fractions of milk from camel and cow are similar in number but differed in migration positions. However, the Western blot analysis of milk proteins from camel showed limited immunological similarities with that from cow (Restani et al. 1999; El-Agamy et al. 2009).

Table 2. Fatty acid profile of milk from alpaca (*Vicugna pacos*), llama (*Lama glama*), guanaco (*Lama guanicoe*), and vicuna (*Vicugna vicugna*) compared with fatty acid profile of milk from an Asian camel, the dromedary (*Camelus dromedarius*).

| Fatty acid (g/100 g of FAME) | South American camelids | | | | Asian camel: dromedary* |
| | Domestic species | | Wild species | | |
	Alpaca	Llama	Guanaco	Vicuna	
4:0	0.07±0.01a	0.08±0.01a	0.05±0.01a	0.14±0.02b	NA
6:0	0.73±0.03a	0.58±0.03b	0.66±0.09ab	0.75±0.06ab	NA
8:0	0.81±0.03a	0.60±0.01b	0.66±0.05b	0.69±0.03b	0.35±0.15
10:0	1.51±0.08a	0.82±0.07b	1.20±0.17a	1.45±0.15ac	0.27±0.12
12:0	0.61±0.04b	0.47±0.03a	0.92±0.09c	0.63±0.05a	3.11±1.09
14:0	11.24±0.65a	12.20±1.22a	10.14±1.20a	10.26±0.28a	12.0±1.8
14:1	1.83±0.12a	3.04±0.33b	2.31±0.32ab	3.10±0.12b	1.70±0.52
15:0	0.13±0.01b	0.12±0.01b	0.89±0.09b	1.65±0.36c	0.75±0.06
16:0	27.19±1.42a	27.98±1.49a	25.80±2.00a	28.43±1.05a	22.8±1.5
16:1	7.99±0.94a	8.22±0.75a	7.08±0.73a	7.93±0.46a	8.30±1.21
17:0	0.45±0.02a	0.52±0.04a	0.61±0.15a	0.53±0.06a	0.55±0.09
17:1	1.37±0.13a	1.25±0.18a	0.85±0.25a	1.13±0.16a	0.76±0.07
18:0	11.42±0.65a	11.12±0.92a	11.38±1.57a	10.13±0.79a	13.83±1.70
18:1 *trans*-11	2.30±0.19a	2.60±0.39ab	2.80±0.33ab	2.98±0.10b	NA
18:1 *trans*-9	1.10±0.09a	1.04±0.11a	1.76±0.13b	1.04±0.14a	NA
18:1 *cis*-9	25.13±1.19a	24.07±2.21a	24.35±2.06a	20.38±2.23a	29.4±2.3
18:2 *cis*-9, *cis*-12	2.39±0.11a	1.47±0.10b	3.81±0.35c	2.74±0.23a	2.83±0.33
18:3 *n*−3	2.06±0.24a	2.05±0.17ac	3.57±0.53b	2.13±0.32a	0.20±0.03
CLA *cis*-9, *trans*-11	1.05±0.08a	1.31±0.13a	1.04±0.10a	1.32±0.12a	0.80±0.15
CLA *trans*-10, *cis*-12	ND	0.08±0.02a	ND	0.08±0.01a	0.06±0.02
22:0	0.37±0.04a	0.14±0.02b	0.12±0.01b	0.08±0.01b	NA
24:0	0.14±0.00a	0.14±0.02a	0.10±0.01a	0.12±0.00a	NA
SFA	54.71±2.11a	54.66±2.84a	52.44±2.16a	54.71±0.77a	55.0±3.0
UFA	45.79±2.13a	45.14±2.80a	47.78±1.77a	42.74±1.92a	NA
MUFA	39.79±2.34a	40.22±2.52a	39.35±1.44a	36.56±2.32a	40.8±2.8
PUFA	5.50±0.22ab	4.92±0.27b	8.42±0.39c	6.18±0.56a	4.26±0.54
SFA/UFA	1.21±0.10a	1.22±0.14a	1.10±0.08a	1.28±0.10a	NA
Atherogenicity index	1.61±0.18a	1.72±0.22a	1.41±0.15a	1.64±0.09a	NA
Desaturase index					
14:1/14:0	0.16±0.03a	0.25±0.03b	0.23±0.05ab	0.38±0.03c	0.14±0.03
16:1/16:0	0.29±0.04a	0.29±0.04a	0.28±0.04a	0.28±0.02a	0.36±0.04
CLA/vaccenic	0.46±0.10a	0.53±0.08a	0.37±0.09a	0.47±0.06a	NA

Note: NA is not available, whereas ND is not determined. Samples were analyzed in duplicate and results are expressed as mean ± SD. Different letters denote significant differences based on Tukey's honestly significant difference (HSD) test ($P < 0.05$).

*Shibani et al. 2011.

The lipid content and the FA composition of milk are the most variable components among mammals, which are affected by factors such as feeding, region, lactation period, and breed (Palmquist 2006; Nantapo et al. 2014). Milk samples assayed in this study belonged to animals from two different regions of Argentina, which enabled us to test for an effect of feeding and climate. Although some individual FA were shown to differ significantly among the four SAC (Table 2), the values were still within the same orders of magnitude indicating a close phylogenetic relationship. Similar proportions of SFA and UFA were also determined for all species. Compared with data available for milk from SAC, we found lower SFA and higher UFA levels in milk from alpaca than those recently reported by Martini et al. (2015). Other authors revealed a FA profile from 14:0 to 18:2 for milk from alpaca with 8% unknown FA (Chad et al. 2014). The proportions of SFA, MUFA, and PUFA from SAC are coincident with data reported for dromedary (Shibani et al. 2011). Our results are also in agreement with the range of FA content reported for old-world camels, including the Bactrian camel (Zhang et al. 2005; Yi et al. 2014) and the dromedary (Konuspayeva et al. 2008; Shamsia 2009). The predominant SFA in milk from SAC were 16:0, 14:0, and 18:0, which are similar to those found in milk from Asian camels (Shibani et al. 2011). However, we found higher levels of 8:0 and 10:0 and a lower level of 12:0 in milk from SAC than in milk from Asian camels (Table 2). This fact implies differences in the specificity of thioesterase in the mammary gland, which is an enzyme associ-

ated with the synthesis of FA with less than 16 carbons in nonruminants (Grunnet and Knudsen 1979).

Among UFAs, the most abundant FA was 18:1 *cis*-9, followed by 18:2 and 18:3. The levels of oleic acid and linoleic acid are coincident with those of Asian camels. We found similar linolenic acid levels to those of the dromedary (Sawaya et al. 1984), but higher than those of the Bactrian camel (Shibani et al. 2011).

The degree to which milk fat originated via de novo biosynthesis of FA by the mammary gland compared with the direct uptake of FA from the diet varies among species. The relative importance of de novo FA synthesis by the mammary gland has generally been regarded as a species-specific characteristic (Iverson and Oftedal 1995). Milk from ruminants differ in the short-chain (4:0–6:0) and medium-chain (8:0–12:0) FA content. Most bovines secrete high proportions of 4:0–12:0 (totaling 10% or more), whereas milk from goat contains up to 27% of these FA (Iverson and Oftedal 1995). The proportion of 16:1 is usually 2% in most Artiodactyla, whereas levels of 18:0 (10%–23%) are higher compared with all other orders.

Short-chain FA levels near 10% were reported for milk from cow and goat (Van Nieuwenhove et al. 2009), but were higher than 12% and 15% for milk from giraffe and red hartebeest (*Alcelaphus caama* (É. Geoffroy Saint-Hilaire, 1803)), respectively (Osthoff et al. 2017).

Compared with ruminants, milk from new-world and old-world camelids contain lower SFA and higher UFA. We found similar 16:0 levels to those in milk from goat and cow from northwestern Argentina (~27% and 1.3%, respectively) (Van Nieuwenhove et al.

2009), which were also similar to 28% for milk from giraffe (Osthoff et al. 2017). A remarkable characteristic of Tylopoda appears to be the extremely high level of 16:1 (8% or more), which suggests a greater desaturase activity in the mammary gland of SAC than in the mammary gland of ruminant. We found similar levels to those of *Camelus* (near 8%; Shibani et al. 2011). Within Artiodactyla, families Suidae (Hrboticky et al. 1990) and Camelidae contain 8% or more 16:1.

Camelids are not considered true ruminants because they have a stomach with three compartments (i.e., pseudo-ruminants), which function like the stomach of ruminants (Wheeler 2012). Therefore, they can digest forage like ruminants because of the symbiotic relationship among microorganisms within this organ, just like the ruminant microbiota. The presence of short-chain FA in the milk from SAC and camel suggests fermentation by this microflora. The short-chain FA absorption at different compartments of the camel forestomach was reported by von Engelhardt et al. (2007). However, compared with ruminants, camelids had a lesser amount of short-chain FA, suggesting differences in fermentation and absorption rates.

The term CLA includes conjugated isomers of linoleic acid that have been produced by the ruminal biohydrogenation process. Another metabolic pathway occurs in the mammary gland throughout the desaturase activity on vaccenic acid (18:1 *trans*-11). Therefore, CLA is mainly found in milk and meat of ruminants, varying according to species and feeding. CLA has been demonstrated to be anti-carcinogenic, an immunodulator, and an anti-atherosclerosis FA (Van Nieuwenhove et al. 2012). The high CLA content of milk from SAC was previously reported for llama (Schoos et al. 2008) and alpaca (Chad et al. 2014; Martini et al. 2015), as well as its precursor, vaccenic acid, that was reported at higher levels in milk from alpaca (Martini et al. 2015). Low CLA content (0.8%) was found in the milk and meat of dromedary (Shibani et al. 2011), but vaccenic acid was not determined. Therefore, both camelids and ruminants presented CLA and vaccenic acid in their milk fat; however, the four SAC had higher CLA and similar vaccenic acid content than ruminants such as goat and cow reared in northwestern Argentina (Van Nieuwenhove et al. 2009).

The high levels of CLA and vaccenic acids and the presence of SCFA confirm the fermentation process in the camelid forestomach, as well as the high CLA desaturase activity in the mammary gland, just like in ruminants.

The myristoleic to myristic ratio indicates the desaturase activity in the mammary gland, because all 14:0 in the milk comes from de novo synthesis produced in this tissue (Lock et al. 2005). The lowest desaturase value was found in alpaca, whereas the highest desaturase value was in vicuna. Our results are coincident with data for llama (Schoos et al. 2008), as well as those for milk from old-world camel (Shibani et al. 2011). Compared with ruminants, the desaturase activity in milk from SAC was at least two times higher than in milk from cow and goat (Van Nieuwenhove et al. 2009; Nantapo et al. 2014).

From a nutritional point of view, milk from SAC could be a healthier food item for humans than milk from old-world camel and ruminant. According to previous studies, the atherogenicity index for milk from cow and goat varied by 2.7 (Van Nieuwenhove et al. 2009) to 5 (Nantapo et al. 2014). Compared with other camelid species, our results are even lower than the value estimated for the genus *Camelus* (Konuspayeva et al. 2008).

Studies on lactation physiology of SAC are very limited. Knowledge regarding the gross composition of milk from wild mammals allows us to understand the nutritional demand of the offspring and its management under different conditions. Our comparative study regarding the composition of milk from alpaca, llama, guanaco, and vicuna is the first to report an interspecific difference between the four species. Human domestication appears not to

have a strong influence on the gross composition of milk from SAC.

Milk from camelid appears to have some distinctive characteristics compared with ruminants: high level of lactose, presence of IgG with heavy chains, lacking β-lactoglobulin, low level of SCFA, high level of UFA, and higher desaturase activity. From a phylogenetic point of view, the proximate composition of milk from SAC appears to be more similar to the Bactrian camel.

Our results contribute new information regarding camelid physiology and provide valuable information in the manipulation of feeding strategies for the management of camelid offspring. The high bioactive lipid content (i.e., CLA), plus the high nutritional quality of the milk, highlight the potential use of milk from SAC as food for humans in poor regions. Therefore, milk production could be exploited as an alternative subproduct of domestic camelid rearing, especially in semi-arid regions of Argentina. Further studies are necessary to establish the general lactation physiology of alpaca, llama, guanaco, and vicuna.

Acknowledgements

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