Changes in Llama (*Lama glama*) Milk Composition During Lactation

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ABSTRACT

Milk samples were collected weekly from 10 llamas during the first 27 wk after parturition under controlled stable conditions. Mean values for the concentrations of the major milk components across the lactation period were 4.70% fat, 4.23% protein, 5.93% lactose, 15.61% dry matter, and 22.62 mg/dL of milk urea N. All constituents were affected by the stage of lactation. There was an increase in fat to protein ratio as protein concentration declined and fat concentration increased. Fat, protein, and lactose concentrations changed during the transition from colostrum to milk. In the first month postpartum, fat concentration remained constant, protein decreased, and lactose increased. Starting with wk 5 postpartum, fat and protein increased and lactose decreased until the end of lactation. Among the major constituents fat had the highest variation. The mean gross energy concentration of milk was 3.88 kJ/g and showed a similar course as protein. Fat contributed 48.0%, protein 26.3%, and lactose 25.7% to the gross energy in the milk. Milk urea N values were higher than those found in ruminants and increased with stage of lactation, whereas the pH decreased. The analyzed milk components were not affected by the lactation number of the animal, except milk urea N. Somatic cell counts indicated the absence of mastitis and revealed that the average somatic cell count of uninfected llamas is lower than in animals usually used for milk production. The 2 algebraic models fitted by a nonlinear regression procedure to the data resulted in suitable prediction curves for the constituents ($R^2 = 0.76$ to 0.94). The courses of major milk constituents in llamas during lactation are similar to those in domesticated ruminants, although different in their values. The established curves facilitate the composition of milk replacers at different stages of lactation for nursing llamas whose dams died or are agalactic.

Key words: llama, colostrum, milk composition, lactation

INTRODUCTION

In its autochthonous regions of South America, the llama (*Lama glama*) is kept as a multipurpose animal for work (transport), wool, and meat. Currently there are about 3.78 million llamas living in South America, mainly in Bolivia and Peru, where they are of major economic and cultural importance for the rural population (Göbel, 2001). Llamas have also been gaining popularity in Europe, North America, and Australia as pet animals and fiber producers. Despite this, there are many gaps in the scientific literature with regard to nutrition, including lactation, in llamas. Contrary to the Old World camels, there is no historic tradition of milking camelids in South America (Bonavia, 1996). There are a few studies on milk composition in llamas (Fernandez and Oliver, 1988; Johnson, 1994; Morin et al., 1995), but to the authors' knowledge no study was published that investigated the major milk constituents across the entire lactation. The most intensive study, by Morin et al. (1995), analyzed milk composition in 83 llamas in the United States, but the samples analyzed were taken during different lactational stages on 8 different farms with a high degree of variation.

During lactation, milk composition undergoes specific changes. In many ungulates rising fat and protein concentrations are accompanied by increasing DM and declining sugar levels (Ofstedal, 1984). The purpose of this study was to examine llama milk composition under a controlled feeding regimen during the course of a 27-wk lactation period and to describe the courses of milk constituents by suitable regression models.

MATERIALS AND METHODS

Animals

In 2 trials, a total of 10 female llamas and their nursing llamas (crias) were involved, originating from the herd of the Experimental Station Relliehausen of Goettingen University and a private German breeder. Animals were transferred 3 mo before parturition for acclimatization and were kept at the Institute of Animal Breeding and Genetics, University of Goettingen, Germany, for a lactation period of 27 wk under controlled stable conditions. Each room measured 5.8×3.2 m, and animals had permanent access to an outdoor pen. In

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Table 1. Characteristics of the lactating llamas and their crias under study

Item	Animal	Age, yr	Weight, kg	Parturition, mo	Sex of cria ¹	Lactation no.
Trial I, July 2004–February 2005						
	1	12	149.0	August	F	7
	2	12	142.0	August	F	6
	3	11	171.5	July	M	5
	4	10	110.0	August	M	6
	5	6	167.0	July	M	1
	6	4	114.0	July	F	1
Trial II, May–November 2005						
	7	5	180.5	May	F	2
	8	5	146.0	May	F	2
	9	9	160.0	May	F	4
	10	8	163.5	May	F	4

¹F = female; M = male.

the stable, light schedule was kept constant (14 h light to 10 h dark). Details of the experimental set-up are given in Table 1. Llama dams were fed twice daily 0.5 kg of a commercial mixed grain and molasses feed containing 16.0% CP, 12.0% crude fiber, 3.0% crude fat, 1.2% calcium, 0.5% phosphorus, 0.3% sodium, 8.5% ash, and 10.2 MJ of ME/kg (HG 58 S, Raiffeisen-AGRAVIS AG, Rosdorf, Germany). Hay from ryegrass-dominated grassland (DM = 860 g/kg of fresh matter; crude ash = 94 g/kg of DM; CP = 131 g/kg of DM; ether extract = 26 g/kg of DM; crude fiber = 283 g/kg of DM; N-free extract = 466 g/kg of DM), water, and mineral feed (HG MIN 13, Raiffeisen-AGRAVIS AG) were available ad libitum.

Milk Collection and Analyses

Colostrum samples were taken 4 to 12 h after parturition. The samples were frozen at -20°C until analysis at the Institute of Veterinary Food Science, University of Giessen, Germany, for fat (Gerber method as outlined in Marshall, 1992), protein (Kjeldahl method as outlined in Marshall, 1992), and lactose (enzymatic method; Kleyn, 1985). The samples were analyzed in duplicate. Because of difficulty handling one of the animals after parturition, only colostrum samples from 9 animals could be obtained. Regular milk samples were then taken at weekly intervals from wk 1 to 27 postpartum (**pp**) from all 10 animals. This time frame was chosen according to the suggested duration of the lactation period of 24 to 28 wk for llamas (Fowler, 1989; Johnson, 1994). Prior to milk sampling, crias and dams were separated for 2 h (1200 to 1400 h); from wk 16 pp, the separation time had to be extended to 3 h (1100 to 1400 h) to obtain an adequate amount of milk necessary for the analysis. Milk let-down was induced by allowing the cria to suckle, except one teat was reserved for the subsequent milk sampling. Two animals always

had to be injected with 1 mL of oxytocin (20 IU/mL) before sampling because they did not allow the udder to be touched while the cria was suckling. The milk sample was then hand-milked from the one teat where the cria was not allowed to suckle, and an effort was made to completely evacuate the gland. The collected amount ranged from 50 to 110 mL.

The samples were filled in test tubes (50 mL) containing 0.05% Bronopol for preservation. The samples were sent immediately in a cooler box at 2°C to the MKU (Milk Control and Research Federation, Uelzen, Germany) and analyzed for the constituents. The maximum time elapsed between sample taking and analyzing was 20 h.

Fat, protein, lactose, fat-free DM (**FFDM**; %), and milk urea concentration (mg/L) were determined by infrared absorption using an infrared spectral-photometer (Milkoscan FT 6500, Foss Electric, Hillerød, Denmark) following the guidelines of good laboratory practice from Lower Saxony (GLP, 2004). For calibration of the infrared spectral-photometer, cow milk was used. Correction factors were calculated by analyzing 10 llama milk samples analytically for fat (Röse-Gottlieb method as outlined in Marshall, 1992), protein (Kjeldahl method as outlined in Marshall, 1992), lactose (enzymatic method; Kleyn, 1985), and urea (Urea test-kit Reflotron, Boehringer Mannheim GmbH, Mannheim, Germany). Somatic cell count was determined using the flow cytometry method with an automated somatic cell counter (Fossomatic 5000, Foss Electric), and pH was measured using a pH meter (inoLab, WTW GmbH, Weilheim, Germany). Gross energy (**GE**) was estimated using the equation after Perrin (1958): $\text{GE (MJ/100 g)} = 39.8 (\text{fat \%}) + 23.9 (\text{protein \%}) + 16.7 (\text{lactose \%})$. The DM concentration of milk was calculated by adding the fat concentration of the milk to the FFDM, and the ash concentration was calculated by subtracting protein and lactose from the FFDM concen-

Table 2. Descriptive statistics for llama milk constituents across the 27-wk lactation period of 10 llamas

Item ¹	Colostrum milk ² (n = 9)	Milk ³ (n = 261)				
	Mean ± SEM	Mean ± SEM	SD	CV	Minimum	Maximum
Fat, %	0.75 ± 0.25	4.70 ± 0.05	0.81	17.29	3.09	6.94
Protein, %	16.79 ± 1.64	4.23 ± 0.02	0.37	8.72	3.36	5.73
Fat:protein	5.44 ± 2.09	111.34 ± 1.24	19.55	17.56	63.67	167.47
Lactose, %	4.12 ± 0.46	5.93 ± 0.02	0.27	4.62	5.18	6.52
DM, %		15.61 ± 0.06	0.94	6.01	13.42	18.44
GE, kJ/g		3.88 ± 0.02	0.34	8.86	3.16	4.91
Ash, %		0.76 ± 0.00	0.01	0.88	0.74	0.77
MUN, mg/dL		22.62 ± 0.39	6.31	27.91	7.93	43.38
pH		6.78 ± 0.01	0.14	2.01	6.40	7.20
SCC, ×1,000/mL		37 ± 2	30	81.68	8	240
logSCC		1.59 ± 0.02	0.27	17.83	0.90	2.38

¹Fat:protein = ratio of fat to protein percentage; GE = gross energy; logSCC = logarithmic-transformed SCC.

²Samples taken 4 to 12 h after parturition from 9 llamas.

³Samples taken from 10 llamas at weekly intervals from wk 1 to 27 postpartum.

tration. Water concentration of milk was estimated calculating $100 - \text{DM}$. Milk urea was converted to MUN (mg/dL) to allow comparison with data from the literature.

For comparing values of milk constituents among species, the present data and results for major milk constituents from the literature were used to calculate the GE concentration in milk applying the equation of Perrin (1958), and values were expressed on a whole milk or GE basis.

Statistical Analyses

All statistical analyses were performed using SAS, version 8.01 (SAS Institute, 1999). There were no significant differences between the 2 trials, and data from both trials were pooled. Variations in the milk composition during the course of lactation were analyzed by the MIXED procedure using a mixed linear model. Because of the repeated measurement, female identity was included as a random effect, and parity, week of lactation, and the trial number were fitted as fixed effects. The SCC were transformed to logarithms to achieve normal distribution (logSCC).

In a preevaluation, 21 different prediction models were fitted to the weekly LSM of constituents by a nonlinear regression procedure (NLIN procedure). On the basis of best fit the following 2 models were chosen that were originally developed to describe lactation curves in cattle:

Model W (Wood, 1967): $Y_w = aw^be^{cw}$, and

Model G (Guo and Swalve, 1997):

$$Y_w = a + bw + cw^2 + dw^3 + e\sqrt{w},$$

where Y_w is the constituent at week w , w is the week pp, e is the Eulerian number, and a , b , c , d , and e are the parameters to be estimated.

The goodness of fit (R^2) and the error mean square (EMS) were used for assessing model adequacy.

RESULTS

Colostrum

Descriptive statistics for fat, protein, and lactose are given in Table 2. As expected for colostrum milk, average protein concentration reached the highest value of the 3 constituents, whereas fat had the lowest. Lactose concentration in the colostrum was lower than in milk.

Composition of Milk

Results for the constituents analyzed are given on a whole-milk basis (Table 2; Figures 1, 2, and 3). In general, parity exerted no significant effect on the constituents with the exception of MUN. However, all analyzed constituents were affected by the stage of lactation ($P < 0.01$), indicating considerable changes in milk composition during the 27 wk of lactation with most changes occurring within 4 wk after parturition.

On a whole-milk basis the fat concentration increased from $4.04 \pm 0.28\%$ in wk 1 to $4.95 \pm 0.27\%$ in wk 27 pp. Among the major constituents analyzed, the highest individual variation was found for fat. On a GE basis, fat averaged $48.0 \pm 0.3\%$ and increased with stage of lactation, from $42.3 \pm 1.6\%$ in wk 1 to $49.5 \pm 1.5\%$ in wk 27 pp.

Protein decreased in the first month from $4.98 \pm 0.11\%$ to $3.80 \pm 0.12\%$ but then steadily increased until the end of the trials to $4.42 \pm 0.12\%$. On a GE basis,

Figure 1. Changes in fat, protein, fat:protein ratio, and lactose of llama milk during the 27-wk lactation period. Data are least square mean values of each week from 10 llamas (■). Curves are based on the algebraic model W (—; Wood, 1967), $Y_w = aw^be^{cw}$, and model G (---; Guo and Swalve, 1997), $Y_w = a + bw + cw^2 + dw^3 + e/w$, fitted to the least squares means by a nonlinear regression procedure, where Y_w is the constituent at week w , w is the week postpartum, and a , b , c , d , and e are the parameters estimated, given in Table 3 together with the corresponding R^2 and EMS.

protein decreased in the first month of lactation from $31.7 \pm 0.8\%$ to $26.7 \pm 0.9\%$ and then remained constant around the average of 26.3% . The fat to protein ratio sharply increased within the first 4 wk from $80.4 \pm 7.0\%$ to $106.0 \pm 7.3\%$ and then reached $111.8 \pm 6.9\%$ until wk 27 pp.

Contrary to fat and protein, lactose increased from $5.78 \pm 0.07\%$ to $6.05 \pm 0.08\%$ in the first month of lactation and then slowly decreased to $5.57 \pm 0.08\%$ (wk 27 pp). On a GE basis, lactose showed a similar course as on a whole-milk basis and averaged $25.7 \pm 0.8\%$. Water concentration followed a similar course as lactose and had slightly increasing values in the first 4 wk of lactation ($84.4 \pm 0.3\%$ to $85.5 \pm 0.3\%$) and decreasing ones for the rest of the lactation period ($84.3 \pm 0.4\%$ in wk

27 pp). Complementarily, DM showed an opposite course and had decreasing values in the first 4 wk pp ($15.61 \pm 0.32\%$ to $14.45 \pm 0.36\%$) and increasing values for the rest of the lactation ($15.68 \pm 0.31\%$ in wk 27 pp).

Gross energy concentration of the milk increased with the stage of lactation from 3.47 ± 0.13 kJ/g in wk 4 to 4.02 ± 0.11 kJ/g in wk 27 pp. The ash concentration had little variation.

The MUN reached the lowest value in wk 5 pp (16.2 ± 1.7 mg/dL) and the highest in wk 26 pp (26.7 ± 1.8 mg/dL). The 2 first-lactation animals had lower ($P < 0.05$) values than animals with more than 1 lactation (19.4 ± 1.4 vs. 22.6 ± 0.6 mg/dL). The mean weekly pH gradually decreased during the lactation and reached its lowest value of 6.60 ± 0.05 at wk 27 pp. Average

Figure 2. Changes in water, DM, ash, and gross energy of llama milk during the 27-wk lactation period. Data are least square mean values of each week from 10 llamas (■). Curves are based on the algebraic model W (—; Wood, 1967), $Y_w = aw^be^{cw}$, and model G (---; Guo and Swalve, 1997), $Y_w = a + bw + cw^2 + dw^3 + e\sqrt{w}$, fitted to the least squares means by a nonlinear regression procedure, where Y_w is the constituent at week w , w is the week postpartum, and a , b , c , d , and e are the parameters estimated, given in Table 3 together with the corresponding R^2 and EMS.

SCC was $37 \pm 2 \times 1,000/\text{mL}$, which is surprisingly low, even though SCC was highly variable (Table 2). The highest weekly average value was observed in the first week with $70 \pm 10 \text{ cells} \times 1,000/\text{mL}$ and the lowest in wk 25 pp with $31 \pm 9 \text{ cells} \times 1,000/\text{mL}$. Results were similar for transformed data ($\log\text{SCC}$).

Prediction Curves

The 2 prediction models for the individual constituents shown in Figures 1, 2, and 3 fitted significantly to the data ($P < 0.01$). The estimated parameters for the 2 models and the corresponding R^2 and EMS are given in Table 3. Both regression models resulted in identical curves for fat, ash, and pH. For all other traits,

the G model with more inflection points than the W model was superior in regard to R^2 and EMS. However, the improvement in terms of R^2 was negligible, except for protein and DM.

DISCUSSION

Colostrum

The llama has epitheliochorial, microcotyledonary placentation, and all passive transfer of Ig occurs after birth through the ingestion of colostrum, explaining the high protein concentration found in the colostrum. Considering the rapid change of protein concentration during the transition from colostrum to milk (Figure

Figure 3. Changes in milk urea N and pH of llama milk during the 27-wk lactation period. Data are least square mean values of each week from 10 llamas (■). Curves are based on the algebraic model W (—; Wood, 1967), $Y_w = aw^be^{cw}$, and model G (---; Guo and Swalve, 1997), $Y_w = a + bw + cw^2 + dw^3 + e\sqrt{w}$, fitted to the least squares means by a nonlinear regression procedure, where Y_w is the constituent at week w , w is the week postpartum, and a , b , c , d , and e are the parameters estimated, given in Table 3 together with the corresponding R^2 and EMS.

1), it is apparent that the Ig concentration diminishes within a few days after birth.

The high protein concentrations in llama milk from 4 to 12 h after parturition as found in the present study are consistent with values reported by Johnson (1994). Similarly, protein values reported for the Bactrian camel and the dromedary are close to 15% (Abu-Lehia, 1989; Zhang et al., 2005). Compared with domestic ruminants, protein concentration in llama colostrum is not markedly different (Hadjipanayiotou, 1995).

The low fat concentration found in the present study compares with reports for the Bactrian camel (Zhang

et al., 2005) and the dromedary (Abu-Lehia, 1989). The higher fat concentrations found for ruminants are assumed to serve as a source of energy for the newborn calf (Merin et al., 2001). In contrast to cattle, suckling in llama crias takes place nearly every hour (Pouillon, 2001) so that no long-term storage of nutritional energy is necessary.

Gross Composition of Milk

For ruminants it is well established that fat is the milk constituent affected most by influences such as feeding, lactational stage, health, etc. (Oftedal, 1984). High variations in the milk fat concentration were also reported for llamas (Morin et al., 1995), but the average value of 4.7% found in the present study is higher than that of 2.7% obtained by the former authors. However, the samples analyzed by Morin et al. (1995) were taken at various lactational stages and from several different locations with feeding practices not reported. The value reported by Fernandez and Oliver (1988) for llamas is in agreement with the present results, but it is unclear at which lactational stages the samples were taken and which diets were fed. Johnson (1994) reported a fat value for llama milk of 5.6%, but the methodology used was not described. For the dromedary, average fat concentrations of 3.6% have been reported (Sawaya et al., 1984), whereas Bactrian camels seem to have somewhat higher average fat concentrations (Zhang et al., 2005). Compared with other domestic ruminants the average fat concentration in llama milk is higher than in goat or cow milk but lower than in sheep milk (Table 4).

None of the published studies examined milk constituents over an entire lactation period for llamas. Only Pouillon (2001) reported weekly values for fat during 22 wk of lactation that did not differ significantly over the measurement period. This course could not be confirmed in the present study because in the first 3 to 4 wk pp the fat concentration remained fairly stable but then increased significantly (Figure 1). The difference could be attributed to the low sample size in the study of Pouillon (2001).

The rather high protein concentration in wk 1 (Figure 1) is probably still attributable to the transition from colostral to normal milk. Similar values for the first week pp were reported by Fernandez and Oliver (1988) and Johnson (1994) for llamas, whereas the value given by Morin et al. (1995) is somewhat lower. The reported results for the alpaca and the vicuña fall within the range of the observed protein concentration (Table 4). Compared with domestic ruminants, only sheep reach similar average protein concentrations, whereas cows and goats have lower values (Table 4).

Table 3. Estimated parameters for milk constituents in llama milk, R^2 , and error mean square (EMS) for 2 algebraic models¹ fitted to weekly least square means of 10 animals

Item ²	a		b		c		d	e	R^2		EMS	
	W	G	W	G	W	G	G		W	G	W	G
Fat	4.0	4.2	-0.01	0.11	0.01	-2E-03	4E-05	-0.25	0.91	0.91	0.011	0.011
Protein	4.8	7.6	-0.15	0.95	0.02	-0.02	3E-04	-3.55	0.84	0.95	0.010	0.003
Fat:protein	84.2	31.0	0.14	-14.8	-0.01	0.30	-3E-03	62.83	0.83	0.88	11.1	7.9
Lactose	5.8	5.1	0.04	-0.24	-0.01	0.01	-8E-05	0.89	0.93	0.94	0.002	0.002
Water	84.6	82.2	0.01	-0.80	-0.001	0.02	-2E-04	2.91	0.82	0.86	0.020	0.015
DM	15.4	17.9	-0.03	0.86	0.01	-0.02	3E-04	-3.07	0.79	0.85	0.023	0.017
Ash	0.8	0.8	0.004	-0.002	-0.001	3E-05	-3E-07	8E-03	0.76	0.76	2E-06	2E-06
GE	3.7	4.3	-0.04	0.02	0.01	-0.004	6E-05	-0.72	0.87	0.88	0.003	0.002
MUN	18.3	24.8	-0.08	3.12	0.02	-0.10	2E-03	-9.03	0.76	0.77	2.3	2.2
pH	6.8	6.8	0.01	-0.01	-0.002	-2E-04	2E-06	0.04	0.94	0.94	4E-04	4E-04

¹Model W: $Y_w = aw^be^{cw}$ (Wood, 1967) and Model G: $Y_w = a + bw + cw^2 + dw^3 + e/w$ (Guo and Swalve, 1997), where Y_w is the constituent at week w , w is the week postpartum, and a , b , c , d , and e are the estimated parameters.

²Fat:protein = ratio of fat to protein percentage; GE = gross energy.

The observed increase in milk fat and protein concentrations during lactation after the first month of lactation is in agreement with observations for many wild and domestic ruminants (Ofstedal, 1984). Contrary to expectation, dromedaries and Bactrian camels are reported to have decreasing fat and protein concentrations over the lactation period (Merin et al., 2001; Zhang et al., 2005).

The development of the fat to protein ratio (Figure 1) revealed that the sudden increase in the first 4 wk pp is attributable to the sharp decline of protein after transition to normal milk. Similar trends were observed in wild and domestic ruminants (Ofstedal, 1984).

The high values for lactose found in the present study are consistent with other findings for llamas (Fernandez and Oliver, 1988; Morin et al., 1995) and their close relatives the alpaca (Medina and Bustinza, 1985) and

the vicuña (Fernandez et al., 1997). Only Johnson (1994) reported a rather low lactose value of 3.30% for llamas, but the methodology applied was not described. Because lactose is the constituent most important to the secretion of the aqueous phase of the milk (Peaker, 1978), milk water tends to increase with increasing lactose values. Similarly, DM concentration decreases with increasing lactose values (Figure 1). Those findings are in agreement with the general observation that species with high milk sugar concentration; for example, in the *Perissodactyla*, have low DM concentrations, whereas species with very low sugar concentrations such as some carnivores or lagomorphs have rather high DM concentrations that may surpass 50%, as in some seals (Ofstedal, 1984).

The average DM concentration found is close to the value of 15.6% reported for llamas by Fernandez and

Table 4. Mean gross energy (GE), DM, fat, protein, and lactose on a whole milk- (WM) and GE-basis obtained in this study and compiled values for alpaca, vicuña, cow, goat, sheep, horse, Bactrian camel, and dromedary

Species	GE, ¹ (kJ/g)	DM	Fat		Protein		Lactose		Source
			WM basis	GE basis ²	WM basis, %	GE basis ²	WM basis	GE basis ²	
Llama	3.9	15.6	4.7	48.0	4.2	26.3	5.9	25.7	Present study
Alpaca	3.5	ng ³	3.2	29.9	3.9	44.9	5.6	25.1	Medina and Bustinza (1985)
Vicuña	4.0	ng	4.6	46.3	3.7	22.4	7.4	31.3	Fernandez et al. (1997)
Cow	3.0	12.4	3.7	49.0	3.2	25.4	4.6	25.6	Ofstedal (1984) ⁴
Goat ⁵	2.7	ng	3.1	46.1	3.1	27.7	4.2	26.2	Min et al. (2005)
Sheep ⁶	4.7	18.2	7.3	61.6	4.1	20.8	5.0	17.7	Ofstedal (1981)
Horse	2.1	10.5	1.3	24.4	1.9	21.4	6.9	54.3	Ofstedal et al. (1983)
Bactrian camel	3.8	14.3	5.7	59.0	3.6	22.4	4.3	18.7	Zhang et al. (2005)
Dromedary	2.9	13.4	3.6	49.7	3.0	24.9	4.4	25.5	Sawaya et al. (1984)

¹Calculated using the equation after Perrin (1958): $GE \text{ (MJ/100 g)} = 39.8 \text{ (fat \%)} + 23.9 \text{ (protein \%)} + 16.7 \text{ (lactose \%)}.$

²Calculated by the present authors.

³Value not given.

⁴Compilation.

⁵Alpine does.

⁶Corriedale ewes.

Oliver (1988). Morin et al. (1995) observed a somewhat lower value of 13.1%. Similar results of 16.3% were also reported for the guanaco (Clavel et al., 2003).

The average ash concentration was in the range of the already published data on llamas and guanacos (Fernandez and Oliver, 1988; Johnson, 1994; Clavel et al., 2003) as well as for camels (Sawaya et al., 1984; Merin et al., 2001; Zhang et al., 2005) and domestic ruminants (Ofstedal, 1984).

By calculating the GE (Table 4) concentration from published milk composition data for llamas using the equation after Perrin (1958), the value found in the present study is in close agreement with Fernandez and Oliver (1988) and Johnson (1998). Only Morin et al. (1995) had a rather low GE value of 2.9 kJ/g, which can be attributed to the low fat concentration found in their study. The average GE concentration in llamas is similar to the milk energy of the other camelids, except the dromedary, which has lower energy concentrations (Table 4). Because fat is the constituent in the milk with the highest caloric value (39.8 MJ/100 g), it is obvious that animals with high fat concentrations have a high GE concentration in their milk (e.g., sheep), whereas animals with low milk fat concentrations such as horses show low GE concentrations (Table 4).

Considering the 3 energy contributors, fat, protein, and lactose, on a GE basis, it is interesting to note that fat contributed on average nearly half (48%) of the GE in the llama milk, whereas protein and lactose comprised the other half almost equally. Compared with domestic ruminants on a GE basis, llama milk seems to be nearly identical to cow milk and close to goat milk, whereas in sheep milk, fat contributes over 60% of the energy. Those findings should be considered when recommendations are given for milk replacers for llamas.

MUN, Milk pH, and SCC of Milk

Urea is the primary form of excretory N in mammals, and BUN is used to evaluate the efficiency of utilization of dietary CP by ruminants (Lewis, 1957). Because urea equilibrates rapidly throughout body fluids, including milk, MUN reflects BUN (Broderick and Clayton, 1997). To the authors' knowledge, no data on MUN have been published for New World camelids, whereas publications on BUN values for llamas range from 13 to 32 mg/dL (Garry et al., 1994). Johnson (1994) reported BUN values of 19.3 and 29.6 mg/dL for llamas consuming diets containing 10 and 16% CP, respectively. The average weekly MUN values of the present study lie within the range of the published BUN data for llamas. Compared with optimum MUN levels from 7 to 14 mg/dL for dairy cattle (Kirchgessner et al., 1986), the reference BUN for llamas or the MUN values in the present

study are considerably higher. The observed high MUN values of 27 mg/dL at the end of lactation would suggest that the animals were then in a slight protein or energy surplus, or both, resulting from a decreasing milk production and a lower CP utilization. This finding could be explained by the fact that animals received 1 kg of concentrate, containing 16% CP, daily throughout the lactation regardless of the lactational stage.

Mean milk pH varies among species from 6.2 to 7.3 (Anderson, 1992). The mean milk pH in the llama (Table 2) seems to be similar to the milk pH in goats (Baldi et al., 2002), although Rowan et al. (1996) reported a somewhat higher value of 6.93 for llamas. The decline of milk pH during lactation in the present study was also observed in the study of Anderson (1992). One explanation for the nearly linear decline may be a reduction of the ability of the mammary gland to produce bicarbonate. Anderson (1992) suggested that milk proteins could be responsible for the pH change in milk because, like blood proteins, they have the ability to control pH as a result of their buffering capacity. But because proteins are more anionic than cationic, an increase in protein concentration should result in an increase in pH. This was not observed in the present study. Another possible explanation is that an increase of organic acids such as citric, acetic, pyruvic, and lactic occurred in the milk.

The observed SCC values in the present study are within the range of the results of an extensive study conducted by Rowan et al. (1996) on udder health in llamas in North America. Compared with animals producing milk for human consumption (e.g., cows, goats, and sheep), llamas have a considerably lower SCC. The major determinant of the SCC in milk is the infection status of the gland (Rowan et al., 1996) and, as observed in the present study, the stage of lactation. Because there were no cases of clinical mastitis in both trials and also no significant effect of parity on SCC, the sole cause for the change in SCC in this study is the stage of lactation.

Prediction Curves

The curves obtained by the 2 nonlinear regression models were similar in shape for protein, GE, and DM. Comparable shapes of curves for protein percentage were also found for cattle (Stanton et al., 1992). The shape of the curves for lactose (Figure 1) and water (Figure 2) percentages are similar to the shape of lactation yield curves, whereas lactose had the best fit aside from protein. The prediction curves for MUN had the lowest fit of all constituents, except for ash. The reason for that is the high variation between the weekly means,

with some outliers especially at wk 5, 8, 11, and 16 pp (Figure 3).

CONCLUSIONS

Peak lactation seems to occur in the llama only for a very short time around the third to fourth week pp (Leyva et al., 1983; A. Riek, unpublished data). Accordingly, the concentrations of milk constituents at around wk 4 pp represent the stage of peak concentration. These findings are consistent with the observations that nursing llamas start to ingest solid food as early as wk 4 to 5 pp (Johnson, 1994; Fowler, 1989), so, from that age, milk is not the only nutritional source. The steady increase of fat, protein (Figure 1), DM, GE (Figure 2) and the decrease of lactose (Figure 1), water, and ash (Figure 2) from wk 4 pp until the end of lactation then describe the rather prolonged late lactation period. For protein percentage a similar trend was observed in dairy cattle, in which the protein percentage curve was inverse to the lactation yield curve (Stanton et al., 1992).

The study showed that milk constituents in llama milk changed considerably over the lactation and were not affected by parity except for MUN.

Both regression models (W and G) applied, although developed to describe cattle milk yield lactation, were suitable to describe the course of the constituents of llama milk over the entire lactation. The differences between the 2 models in terms of model adequacy (R^2) were small, so that for simplicity, the W model, although with less inflection points than the G model, seems adequate to describe the course of the constituents. These estimates may serve as a useful reference to establish standard values for the formulation of milk replacers at different stages of lactation for llama crias whose dams died or have agalactia under European housing conditions with low to medium feeding intensity. But because information on llama milk constituents is limited, especially over the entire lactation period, more systematic studies under different climatic and feeding conditions are needed.

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