INTRODUCTION

Origin and Taxonomy of South American Camelids

Originally the *Camelidae* evolved in North America. From there they migrated into Asia and South America during the Ice Age (Mason, 1979). The dromedary (*Camelus dromedarius*, Linneaus, 1758) and the Bactrian camel (*Camelus bactrianus,* Linneaus, 1758) are the descendants of the wild ancestors that migrated into Asia.

In South America two wild forms, the vicuña (*Vicugna vicugna*, Molina, 1782) and the guanaco (*Lama guanicoe*, Müller, 1776) descended from a common ancestor around two million years ago (Stanley et al., 1994). While the vicuña until recently was assumed never to have been domesticated, the alpaca (*Lama pacos*, Linneaus, 1758) and the llama (*Lama glama*, Linneaus, 1758) are believed to have been domesticated from the guanaco. However, their evolutionary origins are debated (Wheeler, 1995). The decimation of traditional llama and alpaca breeds during the time of the Spanish conquest and the probable subsequent hybridization of the remaining animals with the two wild forms makes a clear interpretation difficult (Kadwell et al., 2001). Mason (1979) places the llama and the alpaca as domesticated species from the guanaco. Kadwell et al. (2001) examined in detail the genetic relationships between South American camelids (SAC), using mitochondrial and microsatellite DNA. Their results suggest that the vicuña is the ancestor of the alpaca and not the guanaco. The authors proposed that the scientific name for the alpaca should be renamed from *Lama pacos* to *Vicugna pacos*. However, despite the high similarity between the alpaca and the vicuña, and between the llama and the guanaco, bidirectional hybridization was also revealed, suggesting that the alpaca could be a hybrid of both the guanaco and the vicuña. Therefore, under the present knowledge it seems not justified to re-classify the alpaca (Table 1).

Table 1. Classification of camelids according to Müller (1961).

Class:			Mammals (*Mammalia*)		
Order:			Even-toed ungulates (*Artiodactyla*)		
Suborder:			Tylopoda (*Tylopoda*)		
Family:			Camelids (*Camelidae*)		
Species:	Guanaco (*Lama guanicoe*)		Vicuña (*Vicugna vicugna*)	Wild camel (*Camelus ferus*)	
	Llama (*L. glama*)	Alpaca (L. *pacos*)		Dromedary (*C. dromearius*)	Bactrian camel (*C. bactrianus*)

Lactation in South American Camelids

Lactation can be seen as the final stage of the reproductive cycle and is related to the physiology of the mammary glands. Lactation starts following parturition and is stimulated by the suckling of the young and lasts, usually depending on the human management, 6 to 9 months until weaning in llamas and alpacas (Bravo, 2002).
The scientific knowledge on the lactation in SAC is very limited. So far there are some published data on milk composition (see Milk composition), none for milk consumption in nursing llamas (crias) and only one on milk output in llamas and alpacas (see Milk output).

Anatomy of the Udder and the Mammary Gland

The udder of SAC is located in the ventral prepubic area between the rear legs and has four short teats, measuring approximately 1 to 2 cm (Figure 1a). An incomplete suspensory ligament of the udder separates the right and left half of the mammary gland (Fowler, 1989). The rear and the front quarter can not be visually or surgically separated, but there is no connection between the collecting system of the two quarters. Each teat has two streak canals that enter into separate teat and gland cisterns, while a variable number of milk ducts collect milk from the gland and empty into the gland cistern (Figure 1b). The teat and mammary gland cistern are not separated and the combined cistern is approximately 2.5 cm long and 1 cm in diameter, which indicates a low storage capacity of the lamoid udder.

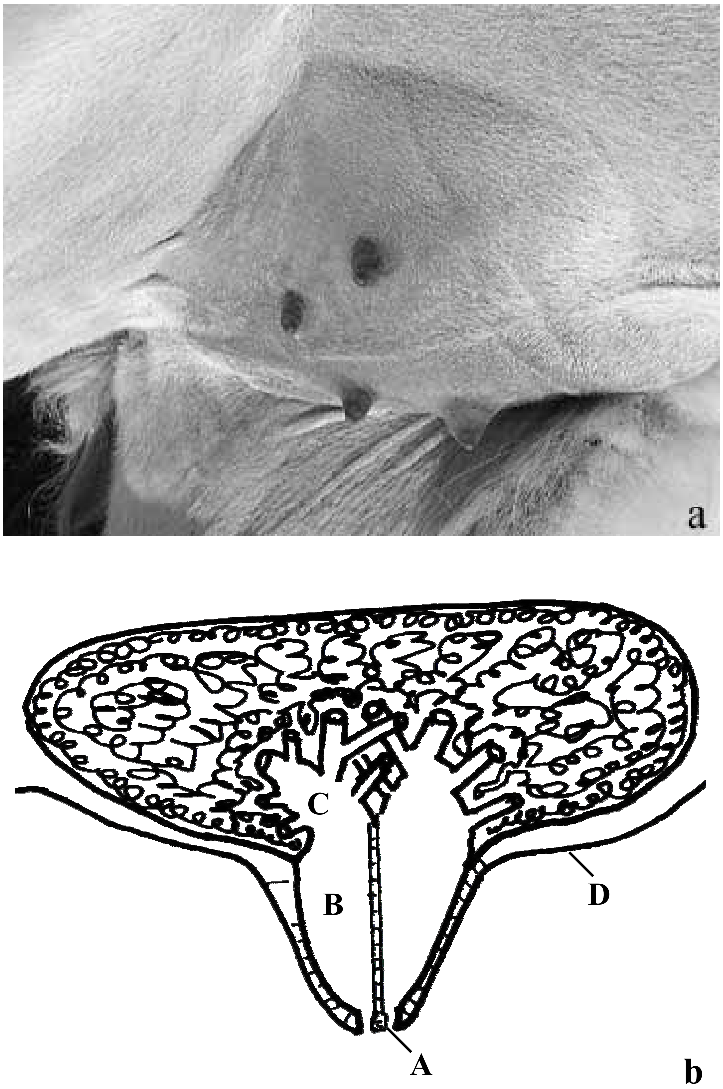

Figure 1. Ventral view of a llama udder (a; photo: Riek) and (b; redrawn from Fowler, 1989) diagram of a llama teat and collection system (A = Streak canal; B = Teat cistern; C = Mammary gland cistern; D = Skin).

Fowler (1989) showed by latex cast preparations and contrast radiography that, although the glands and milk ducts draining into a single teat, overlap and interdigitate with one another, they are separate and distinct with no anastomosis, which results in two mammary glands per quarter and eight altogether. This fact is especially important in the clinical management of mastitis. The glands are compound tubuloalveolar glands similar to those of cattle (Fowler, 1989).

Milk Composition

Milk composition data in SAC are scarce compared to many other species (Jenness and Sloan, 1970; Oftedal, 1984). To the author's knowledge data from six published sources are available for the llama, two for the alpaca and only one for the vicuña and the guanaco (Table 2). However some data are questionable due to the low sample size (König, 1904; Jenness and Sloan, 1970). There are wide discrepancies between the different studies regarding the percentages of the constituents. Especially the fat content in the llama ranges from as low as 2.4 % to as high as 7.3 %. However, fat is the milk constituent mostly affected by various influences such as feeding, lactational stage, health etc. Furthermore milk fat in mammary contents is unequally distributed in many species, which can bias the results either if mammary evacuation during milk collection is incomplete or residual milk after suckling is collected (Oftedal, 1984). As fat is with 39.8 kJ/g the major energy contributor in milk, on a gross energy (GE) basis fat supplies in most studies nearly half of the GE in milk. Regarding the fat content of the other three species in Table 2, fat ranges in the same magnitude as in the llama.

Protein content in SAC milk seems to range around 4 %. Only the studies of Jenness and Sloan (1970) on llama milk and Parraguez et al. (2003) on alpaca milk showed fairly high values of over 6 %. This difference is difficult to explain. Depending on the percentages of the other two energy contributors fat and lactose, protein seems to contribute around 30 % to the gross energy in llama milk (excluding the one sample of Jenness and Sloan, 1970).

Compared to ruminants, llamas seem to have fairly high milk lactose concentrations ranging from 5.6 to 6.5 % (excluding the value from Johnson, 1994). This rather high sugar content is only comparable to that of horses and is also found in the alpaca and the vicuña. Although, the lower value of 4.4 % found by Parraguez et al. (2003) for alpacas kept at the Andean high plateau suggests that the lactose concentration in milk could be affected by feeding resources and altitude. Oftedal (1984) pointed out that species synthesizing lactose in substantial quantity would be expected to secrete milks high in water and low in dry matter content, as lactose appears to be central to the secretion of the aqueous phase of milk. That means that animals with high lactose contents secret milk with high water and low dry matter content. This compares well to the relatively low dry matter concentrations reported for the llama (excluding the one sample of Jenness and Sloan, 1970) and could be an explanation for the higher dry matter and lower lactose concentration in the study of Parraguez et al. (2003) in the alpaca.

Table 2. Published data on milk composition in New World camelids: Gross energy (GE)[1], dry matter (DM), fat, protein and lactose on a whole milk- (WM) and GE-basis[2].

Species	N	GE[1] (MJ/kg)	DM	Fat		Protein		Lactose		Source[3]
				WM-basis	GE-basis[2]	WM-basis	GE-basis[2]	WM-basis	GE-basis[2]	
			(%)	(%)	(%)	(%)	(%)	(%)	(%)	
Lama	3	3.14	13.5	3.2	41	3.9	30	5.6	30	König (1904)
	1	3.44	16.2	2.4	28	6.2	43	6.0	29	Jenness and Sloan (1970)
	30	3.86	15.6	4.7	48	4.2	26	5.9	26	Fernandez and Oliver (1988)
	6	3.85	13.8	5.7	59	4.3	27	3.3	14	Johnson (1994)
	83	2.97	13.1	2.7	36	3.4	27	6.5	37	Morin et al. (1995)
	47	-	n.g.	7.3	-	4.4	-	n.g.	-	Pouillon (2001)
Alpaca	24[4]	3.90	16.8	3.8	39	6.9	42	4.4	19	Parraguez et al. (2003)
	18[5]	3.46	18.8	2.6	30	6.5	45	5.2	25	
	-	3.14	n.g.	3.2	41	3.9	30	5.6	30	Medina and Bustinza (1985)
Vicuña	15	3.95	n.g.	4.6	46	3.7	22	7.4	31	Fernandez et al. (1997)
Guanaco	8	-	16.3	5.8	-	4.4	-	n.g.	-	Clavel et al. (2003)

[1]Calculated using the equation after Perrin (1958): GE (MJ/100 g) = 39.8 (fat %) + 23.9 (protein %) + 16.7 (lactose %). [2]Calculated by the present author. [3]Data are taken from various lactational stages. [4]Samples from animals at the Andean high plateau. [5]Samples from animals in Patagonia. n.g. = not given.

It is widely known that milk composition in many species varies according to lactation stage (Oftedal, 1984). However, the degree and direction of that change is different among species. In all studies presented in Table 2, samples were pooled from different lactation stages and animals. In the most comprehensive study, done by Morin et al. (1995), milk samples were collected from different lactational stages and 8 different farms in the United States. Parraguez et al. (2003) collected monthly milk samples over a five months lactation period in alpacas kept at the Andean high plateau and in Patagonia, however no clear trend of the course of the constituents was apparent. To date no study has investigated the change of milk composition in llamas over the entire lactation, except in the study of Pouillon (2001). However, in that study only fat and protein were analysed and the weekly sample size varied between 1 and 5 samples. The lactational stage had no significant effect on fat and protein content in the milk.

Milk Output

To the author's knowledge, there is only one published study on llama milk output. Bravo (2002) reported daily peak yields of 2.35 l at week 3 pp for the llama and 1.94 l for the alpaca at week 2 pp. However, the data were redrawn from Leyva et al. (1987) with no comment on how many animals were included in the study or which methodology was used to measure the milk yield.

Estimation of Milk Intake

In order to gain information or give recommendations on nutrient intakes of young during lactation, not only the composition of milk is of interest but also the amount of milk ingested by the young. Sometimes lactation studies focus on suckling behavior as a positive estimate of milk transferred (Clutton-Brock et al., 1982; Gauthier and Barrette, 1985). However those estimates are suspect, as the relationship between milk transfer and suckling behavior is only weak (Cameron, 1998; Cameron et al., 1999). Thus, to measure milk intake in young several methods have been developed.

'Test-weighing' Procedure

The procedure has been widely used for various species. The method involves the weighing of the young before and after an induced suckle event, with the difference of the two weights assumed to be the milk ingested by the young. That implies that the mother animal and the young are kept under stable conditions in order to induce a timed suckle event. However various possible errors associated with the 'test-weighing' procedure have been discussed (Doney et al., 1979). Possible errors lie in the urination and defecation of the young during suckling or that the amount of milk ingested by the young after a timed and controlled suckle event does not equal the amount of milk ingested if milk consumption occurs in an undisturbed environment (Oftedal, 1981). Both sources of errors are difficult to avoid in many young. Prevention of frequent suckling may result in a reduction of milk produced by the mother (Linzell, 1972; Hanwell and Linzell, 1973; Cross, 1977) or the accumulation of amounts of milk in the udder that young are unable to consume (McCance, 1959; Doney et al., 1979). Attempts to make weight corrections for the urination and defecation during a suckle event have been shown to be difficult (Arman et al., 1974; Sadleir, 1980). Therefore reliable results can only be obtained if the intersuckling-intervals employed are similar to normal suckling patterns, young do not urinate or defecate during a suckle event and the separation of mother from young (or other means to prevent suckling) are accomplished with minimal stress for the animals. However, young with high suckling frequencies and short suckling duration, e.g., pigs and llamas consume small amounts of milk during a suckle event, thus the weighing error increases with decreasing amounts of milk ingested and increasing weight of the young (Garcia et al., 1999).

Timed Milking

This method is used to measure indirectly the milk taken in by the young by emptying the udder both before and after a timed interval during which the young are prevented from suckling. The amount collected at the second milking is assumed to represent the amount secreted over the timed interval. The method has been mainly applied to cattle and sheep (McCance, 1959; Cross, 1977) but also in red deer (Landete-Castillejos, 2001). However, to be accurate the method implies a complete evacuation of the udder at each timed milking interval and frequently the application of exogenous oxytocin. Especially animals with a high proportion of milk stored in the mammary alveoli and ducts (e.g., wild ruminants) rather than sinuses and cisterns (e.g., domestic ruminants) are difficult to milk out completely and may require exceptionally large doses of oxytocin (Oftedal, 1981). Furthermore the animals need to be tame and used to the milking procedure. This method is therefore hardly applied in non-dairy species due to the difficulty in achieving mammary evacuation.

Isotope Dilution Technique

The isotope dilution technique to measure milk intake in suckling young involves the application of an isotope to the young, with hydrogen isotopes being the most common isotopes used (^{2}H = Deuterium in $^{2}H_2O$ = Deuterium oxide and ^{3}H = Tritium in $^{3}H_2O$ = Tritiated water). However, Kametake (1974) and Green and Newgrain (1979) used ^{42}K and ^{22}Na to measure the isotope turnover in suckling young.

Deuterium oxide (^2H_2O) is a stable and relatively non-toxic isotope. Pinson (1952) showed in mice, that up to 25 % of total body water can be replaced by deuterium oxide before toxic effects occur. Tritiated water instead (^3H_2O) is a weak radioactive beta emitter with a long half life (12 years).

The method was first proposed by Macfarlane et al. (1969) and since then was used to estimate milk intake in many species (see Chapter 5, Table 1). If milk is the sole source of water for the young then the fractional water turnover, measured by the mono-exponential decline of the isotope water in body fluids, is a measure of milk water ingested. Several validation studies showed that milk intakes measured by bottle or bucket feeding were in good agreement with milk intakes estimated by the dilution procedure (Table 3). The data in Table 3 show that especially in the first decades after the publication of the results from Macfarlane et al. (1969) mainly tritium was applied instead of deuterium, as at that time the availability of a high resolution mass spectrometer capable of analysing small differences in deuterium, such as those found in natural water supplies was not given. Today deuterium can easily be measured in natural tape water, indicating the high resolution capability of today's mass spectrometers making it no longer necessary to apply tritium or large doses of deuterium.

After administration of isotopic water to the young (orally, intramuscularly or intravenous), labelled water mixes rapidly with body water (Coleman et al., 1972). After mixing any body fluid (blood, urea, saliva etc.) can be assayed for isotope determination. Blood, urine and saliva have been used but blood sampling usually avoids most potential problems of contamination or evaporation during collection (Oftedal and Iverson, 1989). A detailed description of the method can be found in the materials and methods section of Chapter 3.

The dilution procedure has the advantage that it can measure the water and therefore the milk intake over a certain time period. However, the assumption is that milk intake is directly related to water intake. It is not possible with this method to differentiate between water ingested from various sources. Since measurement of feed and water intakes under field conditions is accompanied with difficulties, the method is only suitable to measure milk intake, if milk is the only water source or if other sources of water ingested can be measured or estimated. Possible errors associated with isotope dilution have been described in detail (Lifson and McClintock, 1966; Nagy and Costa, 1980; Oftedal and Iverson, 1989).

One assumption of the method implies that the water intake and excretion over the measuring period is constant, however that depends on the suckling frequency of the young. Animals with high suckling frequencies such as piglets, lambs or suckling llamas are less prone to errors than animals with periodic bouts of milk intake e.g., seals where the water turnover rate is not constant but fluctuates in response to infrequent intake (Oftedal et al., 1987). In general, the more continuous suckling bouts occur the shorter the measurement period can be chosen (Oftefdal and Iverson, 1989). A further assumption is that isotopic water labels body water only and is not incorporated into body tissue, which is generally the case (Oftedal and Iverson, 1989). However, a rapid exchange between small amounts of isotope with unstable hydrogen in organic molecules (e.g., proteins) can overestimate total body water. Theoretically this could amount to 4 % of the dilution space (Culebras and Moore, 1977). Though comparative carcass analysis, measuring total body water directly were in good agreement with the estimations by the dilution procedure (Pinson, 1952; Panaretto, 1968; Houseman et al., 1973; Sheng and Huggins, 1979; Odwongo et al., 1984; Schoeller et al., 1985; Bowen and Iverson, 1998).

Another source of error is the recycling of hydrogen isotope from the young to the mother and back to the young by maternal intake of infantile urine or faeces and the resulting excretion of the recycled isotope with the milk. This is mainly the case for animals with many young (e.g., pigs, dogs, rats etc.). A possibility to overcome that problem is to leave one animal per litter unlabeled as a control (Baverstock and Green, 1975).