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Does the Milk of Callitrichid Monkeys Differ From That of Larger Anthropoids?

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The generalization that anthropoid primates produce dilute milks that are low in protein and energy is based primarily on data from large monkeys of the families Cebidae and Cercopithecidae, as well as humans. The marmosets and tamarins (Callitrichidae) are not only much smaller in body size, but also typically raise multiple offspring during a relatively brief lactation. We hypothesized that selection for small body size and high reproductive rate might favor secretion of milk of higher energy and protein concentrations. To test this hypothesis, 46 milk samples collected from 10 common marmosets (*Callithrix jacchus*, ca. 350 g) were assayed for dry matter (DM), crude protein (CP), fat, and sugar; and gross energy (GE) was calculated from these constituents. We also assayed five samples collected from three golden lion tamarins (*Leontopithecus rosalia*, ca. 700 g) and six samples collected from a single pygmy marmoset (*Cebuella pygmaea*, ca. 150 g) over two lactation periods. All samples were collected between days 10 and 57 post partum, representing mid lactation for these species. The milks of these three species were similar, containing 14.0%, 16.1%, and 13.7% DM; 2.7%, 2.6%, and 2.9% CP; 3.6%, 5.2%, and 3.7% fat; 7.4%, 7.2%, and 7.8% sugar; and 0.76, 0.90, and 0.82 kcal/g for common marmosets, golden lion tamarins, and the pygmy marmoset, respectively. These species produced milks with energy values that were within the range reported for large anthropoids, albeit with slightly higher protein concentration. However, milk composition did vary substantially among individual common marmoset females, especially in the proportion of milk energy derived from fat. In contrast, CP as expressed as a percent of GE was remarkably constant among common marmoset females. Callitrichid milk appeared to be similar to that of larger anthropoid primates in GE, but was higher in CP and in the proportion of GE from CP. However, the small sample sizes for the golden lion tamarin and the pygmy marmoset, and the wide variation in milk composition found among common marmoset females cautions against definitively characterizing the milks of callitrichids from these data. Am. J. Primatol. 56:117–127, 2002.

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INTRODUCTION

Although anthropoid primates typically produce dilute milks with low levels of fat, protein, and gross energy (GE), fragmentary data from a few cebids and callitrichids suggest that their milks may be more concentrated [Oftedal, 1984]. Blaxter [1961] proposed many years ago that small neonates should require more energy-dense milk since energy requirements are proportional to metabolic body size (mass to the power 0.75), whereas gastrointestinal capacity is directly proportional to body mass [Oftedal et al., 1989]. If milk intake is proportional to gastrointestinal capacity, energy density of milk should be proportional to $M^{0.75}/M^{1.0} = M^{-0.25}$ [Payne & Wheeler, 1968]. However, an allometric comparison among primates is complicated by the fact that most anthropoid milk composition data are for large-bodied species, such as macaques, baboons, and howler monkeys. The extent to which samples obtained in previous studies are representative has also been questioned [Oftedal, 1984; Oftedal & Iverson, 1995]. For example, Oftedal [1984] concluded that early studies of the milks of squirrel monkeys, marmosets, and tamarins [Buss & Cooper, 1972; Buss, 1975; Turton et al., 1978] did not warrant inclusion in a review of mammalian milks. These studies encompass just a few samples collected at different stages of lactation and in some cases after the death of the infant. More recently, a study of 13 prosimian species demonstrated considerable variation among genera in milk composition, but this was attributed to pattern of maternal care, not body size [Tilden & Oftedal, 1997].

An understanding of interspecific variation in milk composition is important not only to interpretation of reproductive strategies, but also in selecting an appropriate milk formula for feeding neonates. For example, it is common to enhance the fat and protein concentrations in human milk formulas if they are to be fed to neonatal callitrichids out of the belief that smaller primates need more concentrated formulas [Oftedal, 1980; Kirkwood & Stathatof, 1992]. Reliable milk composition data are needed to verify this view.

The New World monkeys in the family Callitrichidae are the smallest of the anthropoid primates. Callitrichids generally have a higher reproductive output than is usual among other anthropoids: twin offspring are the norm, with two litters per year not uncommon. The gestation ranges from 128 to 180 days [Hartwig, 1996] and is followed by a relatively short lactation period: infants begin to eat solid food by 1 month and are weaned at or before 3 months [Hearn, 1983]. In many species females will become pregnant within weeks of parturition [Tardif, 1994]. Thus, callitrichid primates appear to have relatively brief but intensive reproductive phases, quite different from the long dependency and low rate of milk energy output characteristic of large anthropoids such as baboons [Roberts et al., 1985]. Allometric considerations, the production of twins, and the brevity of lactation all suggest that a rapid rate of nutrient transfer from mother to young may be essential to reproduction in callitrichids. If so, there may be a selective advantage to production of milk high in energy and nutrient composition.

The common marmoset (*Callithrix jacchus*) is among the smallest of the Callitrichidae (ca. 350 g), and has a rate of reproductive output that is not surpassed by any other callitrichid species. Females typically ovulate within 14 days post partum [Tardif & Bales, 1997], so that females are commonly pregnant during lactation [Hearn, 1983]. Thus, if milk composition of callitrichids were to vary from that of other anthropoids based on the small body size and high reproductive rate, the common marmoset would be a prime candidate to display this trait. We predicted that common marmoset milk would be higher in dry matter (DM), fat, protein, and GE than the milks of larger primates. Milk samples were obtained from 10 common marmoset females *Callithrix jacchus*. Opportunistic milk samples were also obtained from two other callitrichid species for comparison: a single pygmy marmoset, *Cebuella pygmaea* (the smallest callitrichid, ca. 150 g), and from three golden lion tamarin females, *Leontopithecus rosalia* (one of the largest callitrichid species, ca. 700 g). This study is part of an ongoing research project investigating the effects of nutrition on reproduction in callitrichid monkeys.

METHODS

Milk samples were collected from 10 captive *Callithrix jacchus* over a 5-yr period at approximately days 20, 32, and 45 post partum during one to four lactation periods (defined as the period of time from the birth of the infant until it is weaned) for each animal. For comparison, milk was also collected from three captive *Leontopithecus rosalia*: a single sample from one female at day 10, a single sample from another female at day 50 post partum, and three samples from a third female at days 20, 42, and 55 of a single lactation period. Samples were also collected from a single captive *Cebuella pygmaea* from two lactation periods at days 20, 32, and 45 post partum. These time periods correspond to mid lactation in these species. In addition, samples from three *C. jacchus* females collected during late lactation (approximately day 75 post partum) were assayed. Callitrichid infants are thought to be completely weaned before 90 days post partum.

All *C. jacchus* were fed, ad libitim, one of two isocaloric, homogenous, gelled, purified diets containing lactalbumin, dextrin, sucrose, soybean oil, cellulose, agar, and vitamin and mineral premixes for the duration of the study (details of the diets can be found in Tardif et al. [1998]). The diets were formulated to provide either 15% or 25% of estimated metabolizable energy (ME) from protein, while keeping other nutrient concentrations the same. Both provided 11% of estimated ME from fat. These two protein levels were chosen to test the hypothesis that the smaller New World monkeys require higher dietary protein concentrations than do Old World anthropoids, as was suggested by the National Research Council [1978] but disputed by one of us [Oftedal, 1991]. The other two species were fed, ad libitim, standard mixed diets, including fruit, vegetables, and minor treat items, but a commercial canned diet that provided approximately 20% of ME from protein (Marmoset Diet, Hill's Food, Topeka KS) provided the major portion of most nutrients. All animals were housed in family groups, with a breeding male and female and their immature offspring.

Females were separated from their infants shortly after emerging from the nest box in the morning, and kept separated for 3–4 hr to allow accumulation of milk in the mammary glands. The marmosets were anesthetized with ketamine hydrochloride and injected IM with oxytocin (2–3 IU). The golden lion tamarins were anesthetized with isoflurane gas and injected IM with 4 IU of oxytocin. The nipples were cleaned with distilled water, and milk was manually expressed into a vial. Efforts were made to completely evacuate both mammary glands. The milk was stored frozen at –20°C until chemical analyses were performed.

Milk samples smaller than 0.35 g were pooled across lactation periods within female and lactation day (e.g., two samples from different lactation periods for animal 003 at day 20 post partum were pooled). All samples larger than 0.35 g were assayed separately. A total of 43 samples of *C. jacchus* mid-lactation milk (six pooled samples and 37 individual samples) and three pooled samples from late lactation were assayed. Six samples of *C. pygmaea* and five samples of *L. rosalia* mid-lactation milk were assayed.

Milk constituents were measured at the Nutrition Laboratory of the Smithsonian Institution National Zoological Park using standard methods [Oftedal & Iverson, 1995]. DM (total solids) was measured gravimetrically after drying for 3 hr at 100°C in a forced-air drying oven. Total nitrogen (TN) was determined by the micro-Kjeldahl method for most of the *C. jacchus* samples, as these were of sufficient volume. Small samples of *L. rosalia* milk were originally assayed by a colorimetric procedure (Nessler's procedure) [Koch & McMeekin, 1924; Oftedal & Iverson, 1995], but the purchase and validation of a CHN elemental gas analyzer (model 2400, Perkin-Elmer, Norwalk, CT) provided a rapid and accurate method of assaying TN in 20-μl milk samples, and was thus used for the *C. pygmaea* samples, some of the *C. jacchus* samples, and the *L. rosalia* sample from 50 days post partum. In our laboratory these methods were each standardized against the macro Kjeldahl procedure (nitrogen recovery 98–99%) and yielded comparable results for cow and other milks. Crude protein (CP) was estimated as 6.38× total nitrogen. Total lipid was measured by sequential extractions with ethanol, diethyl ether, and petroleum ether by a micro modification of the Rose-Gottleib procedure for the common marmoset and golden lion tamarin samples, and for the three of the six samples from the pygmy marmoset for which there was sufficient sample. Total sugar was assayed by the phenol-sulfuric acid method, using lactose monohydrate as the standard [Dubois et al., 1956; Marier & Boulet, 1959], with the results expressed on an anhydrous lactose basis. GE was calculated per Oftedal [1984], assuming nonprotein nitrogen of 0.04% by analogy with human milk. Assays were performed in duplicate whenever sample volume was sufficient (for *C. jacchus*, 32/46 samples had duplicate assays for CP, 41/46 for fat, and 46/46 for sugar).

Results are expressed as the mean ± standard error. Sample size was sufficient in *C. jacchus* to examine the relationships among the milk constituents by Pearson product-moment correlation. The variation in DM, CP, fat, sugar, and GE concentrations of *C. jacchus* milk was examined by multivariate analysis of covariance, with individual and diet (15% and 25% ME from CP) as the categorical variables, and days post partum as the covariate. Differences in amount collected, and DM, CP, fat, sugar, and GE concentrations of *C. jacchus* milk between mid and late lactation were examined using one-way multivariate analysis of variance.

RESULTS

The DM of individual *C. jacchus* mid-lactation milk samples ranged from 11.0% to 24.4%, fat from 0.7% to 12.9%, CP from 1.9% to 5.1%, and sugar from 4.9% to 9.3%. Fat, CP, and sugar accounted for 98.4% ± 1.1% of DM on average. The estimated GE of *C. jacchus* milk ranged from 0.53 to 1.67 kcal/g. The mean values for each female *C. jacchus* are presented in Table I. The protein concentration of the diet did not affect milk composition. Days post partum did not affect mid-lactation milk DM, CP, fat, or GE, but sugar concentration decreased over lactation (Table II). Fat and CP were positively correlated with each other and with milk DM and GE, while sugar concentration was negatively correlated with the other constituents (Table II). The proportion of GE from protein was fairly constant among females at 19.0% ± 0.7% (F = 1.90, df = 9,33, P = 0.087), when compared with the proportions of GE from fat (F = 2.87, df = 9,33, P =

TABLE I. Average Values for Milk Constituents for Mid-lactation Milk by Female for Ten Common Marmoset Monkeys (*Callithrix jacchus*)

Animal	N[a]	n[b]	DM (%)	CP (%)	Fat (%)	Sugar (%)	GE (kcal/g)
15% CP	Diet						
002	2	6	15.7 ± 1.2	2.9 ± 0.2	4.7 ± 0.5	7.1 ± 0.2	0.87 ± 0.05
003	3	3	13.7 ± 0.7	2.5 ± 0.1	3.5 ± 0.9	7.2 ± 0.0	0.74 ± 0.08
018	4	5	12.5 ± 1.3	2.7 ± 0.1	2.3 ± 0.6	7.4 ± 0.2	0.65 ± 0.05
030	4	9	15.9 ± 1.2	3.3 ± 0.3	5.2 ± 1.0	7.0 ± 0.3	0.93 ± 0.10
032	3	6	14.2 ± 0.6	2.7 ± 0.1	3.1 ± 0.6	8.0 ± 0.3	0.75 ± 0.05
035	1	2	11.9 ± 0.9	2.1 ± 0.2	2.3 ± 0.3	7.9 ± 0.5	0.63 ± 0.05
Average			14.0 ± 0.7	2.7 ± 0.2	3.5 ± 0.5	7.4 ± 0.2	0.76 ± 0.05
25% CP	Diet						
013	2	3	14.2 ± 1.2	3.1 ± 0.1	3.7 ± 0.8	6.6 ± 0.1	0.77 ± 0.07
015	1	3	15.6 ± 1.2	3.1 ± 0.2	5.3 ± 0.6	7.4 ± 0.2	0.95 ± 0.05
024	1	2	13.8 ± 1.2	2.1 ± 0.2	4.2 ± 0.5	7.3 ± 0.1	0.78 ± 0.04
028	2	4	12.5 ± 0.6	2.6 ± 0.2	2.1 ± 0.4	7.7 ± 0.2	0.63 ± 0.04
Average			14.0 ± 0.6	2.7 ± 0.2	3.8 ± 0.7	7.3 ± 0.2	0.78 ± 0.07
Average all samples			14.0 ± 0.4	2.7 ± 0.1	3.6 ± 0.4	7.4 ± 0.1	0.77 ± 0.04

[a]N, number of lactation periods.
[b]n, number of milk samples.

0.013) and sugar (F = 3.596, df = 9,33, *P* = 0.003). Females with lower GE milk had a higher proportion of milk energy from sugar, while females with high GE milk had a higher proportion of milk energy from fat (Fig. 1).

Only three *C. jacchus* females (003, 002, and 030) produced sufficient milk at day 75 post partum for analyses to be performed, and the average amount of milk collected at day 75 from these females was significantly less than from earlier in lactation (0.14 ± 0.04 g, n = 8, vs. 0.39 ± 0.05g, n = 23, respectively; F = 6.818; df = 1,29; *P* = 0.014). Day 75 samples had to be pooled within female from

TABLE II. Pearson Product–Moment Correlation Coefficients Between Days Post Partum and the Dry Matter (DM), Crude Protein (CP), Fat, Sugar, and Gross Energy (GE) Content of Mid-lactation Common Marmoset Milks

	Days post partum	DM	CP	Fat	Sugar
Days post partum	–				
DM	r = .002 *P* = .992 n = 42	–			
CP	r = .173 *P* = .267 n = 43	r = .750 *P* < .001 n = 42	–		
Fat	r = .082 *P* = .600 n = 43	r = .883 *P* < .001 n = 42	r = .646 *P* < .001 n = 43	–	
Sugar	r = –.343 *P* = .024 n = 43	r = –.551 *P* < .001 n = 42	r = –.632 *P* < .001 n = 43	r = –.618 *P* < .001 n = 43	–
GE	r = .062 *P* = .693 n = 43	r = .911 *P* < .001 n = 42	r = .709 *P* < .001 n = 43	r = .991 *P* < .001 n = 43	r = –.567 *P* < .001 n = 43

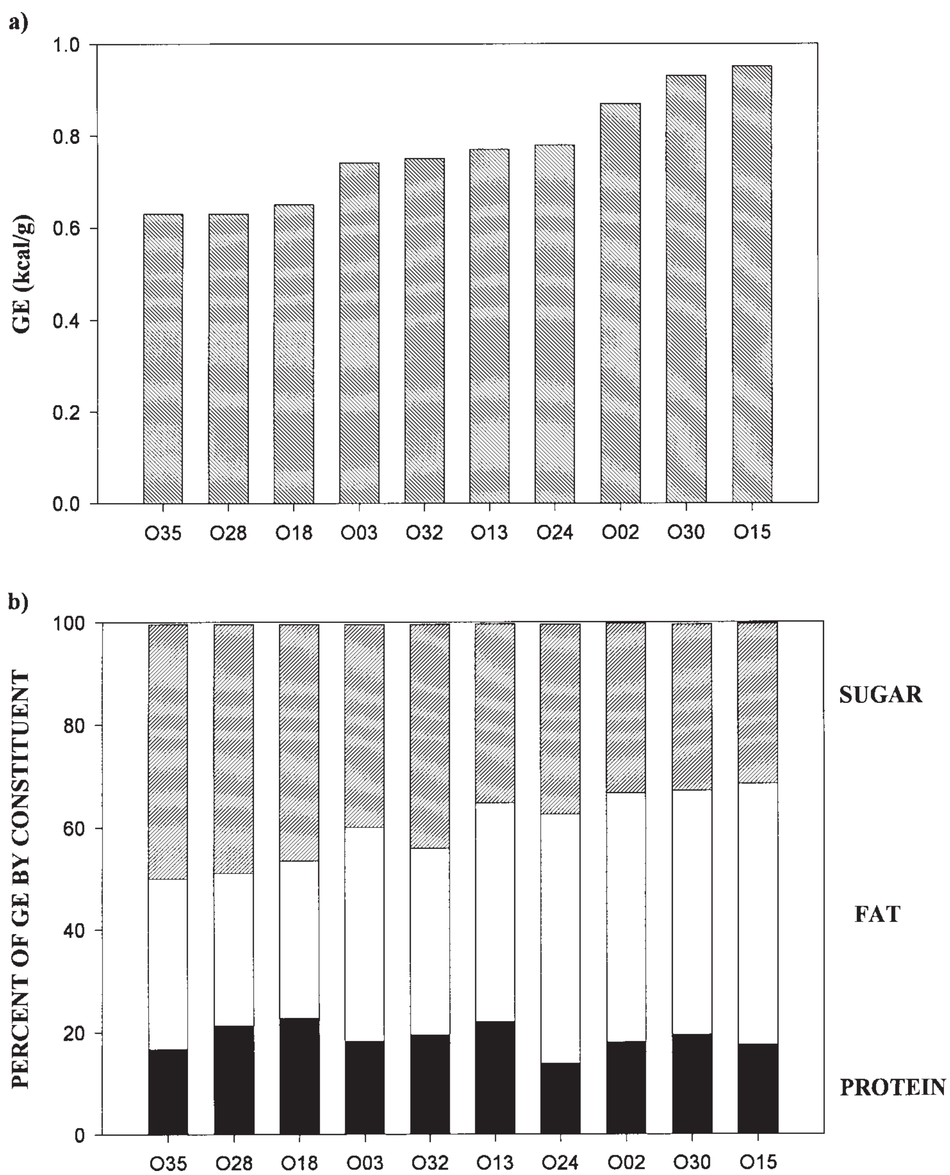

Fig. 1. **a:** Mean GE of milks for individual *Callithrix jacchus*. **b:** Proportion of milk GE from protein, fat, and sugar for *C. jacchus* individuals.

two or more lactations to be sufficient for analyses. Mean DM (14.8% ± 0.9%), fat (3.9% ± 0.8%), and CP concentrations (3.6% ± 0.2%) of day 75 post partum samples were not different from mid-lactation values, but sugar (5.9% ± 0.4%, n = 3 for late lactation vs. 7.1% ± 0.2%, n = 18 for mid lactation) was lower (F = 8.433; df = 1,19; P = 0.009).

The milk of the pygmy marmoset was similar to that of *C. jacchus* in DM, fat, CP, and GE (Table III). The milk of *L. rosalia* also was similar to that of the common marmosets on average (Table III). One of the golden lion tamarin fe-

TABLE III. Average Values for Milk Constituents for Mid-lactation (10–55 Days Post Partum) Milk by Female for a Single Pygmy Marmoset (*Cebuella pygmaea*) and Three Golden Lion Tamarins (*Leontopithecus rosalia*)

Animal	n[a]	DM (%)	CP (%)	Fat (%)	Sugar (%)	GE (kcal/g)	% GE (CP)[b]
C. pygmaea							
Gemini	6[c]	13.7	2.9	3.7	7.8	0.80	19.3
L. rosalia							
Emily[d]	1	14.8	2.7	2.4	7.3	0.65	21.9
Cleo[d]	3	21.0	3.0	11.2	6.7	1.45	11.1
Siena	1	12.4	2.2	2.1	7.6	0.61	18.7
Average		16.1	2.6	5.2	7.2	0.90	17.3

[a]n, number of milk samples.
[b]Percent of estimated gross energy from protein.
[c]Two lactation periods; n = 3 for fat and for energy values.
[d]These data were also reported as unpublished data in Oftedal & Iverson [1995].

males, however, produced a higher-fat milk than was typical for the other callitrichids in this study, although it was within the range of values found for individual common marmoset samples (see above).

DISCUSSION

Oftedal and Iverson [1995] list 16 species of nonhuman primates for which gross milk composition data are available for at least three samples of mid-lactation milk. Large-bodied anthropoid species (from the genera *Alouatta*, *Cercopithecus*, *Macaca*, *Papio*, and *Homo* [Oftedal, 1984]) produce dilute milks that are low in protein (<2.5%) and fat (<5.5%), and relatively high in sugar (>6%). Among large-bodied prosimian species, *Eulemur* produce dilute milks (CP = 1.3%, fat = 1.0%, and sugar = 8.5%), but *Varecia variegata* does not, rather producing milk with a higher protein concentration (4.2%) [Tilden & Oftedal, 1997]. The small prosimians for which there are reliable data (*Otolemur garnettii*, *O. crassicaudatus*, and *Nycticebus coucang*) produce milks that are higher in fat (7–8%) and protein (3.9–5.2%) than is typical for large anthropoids and *Eulemur* [Tilden & Oftedal, 1997].

However, body size does not appear to be a satisfactory or consistent explanation for the variation in milk energy density among primates. Callitrichids, the smallest anthropoid species, produce milks similar in GE to that of larger anthropoids (Table IV). Moreover, the range in mean GE (0.63–0.95 kcal/g) among the *C. jacchus* individuals in this study (Table I) was comparable to the range among primates listed in Table IV. The sources of variation in the milk of *Callithrix jacchus* are poorly understood, but appear to include an effect of maternal condition. The combined effects of maternal size and litter size also may play a role, as smaller mothers of twins produce lower energy milks [Tardif et al., 2001]. Dietary protein concentration, however, did not affect milk composition.

Although similar in energy content, callitrichid milks in this study were significantly higher in protein than the milks of other anthropoids listed in Table IV (2.7% ± 0.1% vs. 1.7 ± 0.2%, $t = 3.639$, $df = 6$, $P = 0.011$). The proportion of GE from protein also was greater in the callitrichids compared to the Old World anthropoids, but, interestingly, not greater than that of the cebid, *Alouatta*. The proportion of milk energy as protein has been suggested to relate to a species' growth rate [Bernhart, 1961], and the low protein content of human milk to relate to the long time to maturation [Powers, 1933]. This correlation breaks down

TABLE IV. Gross Energy (GE), Crude Protein (CP), and Percentage of Calories From Protein in the Milks of Primate Genera for Which There Are Comparable Data

Family	Genus	n[a]	GE (kcals/g)	CP (%)	Percent of GE from CP	Reference[b]
Hominidae	*Homo*	99	0.61	0.9	5.9	1
Cercopithecidae	*Papio*	24	0.79	1.5	9.2	2
	Macaca	35	0.80	1.8	11.6	2
	Cercopithecus	4	0.67	2.1	16.2	2
Cebidae	*Alouatta*	14	0.49	2.0	21.3	2
Callitrichidae	*Callithrix*	43	0.77	2.7	19.0	3
	Cebuella	6	0.80	2.9	19.3	3
	Leontopithecus	5	0.90	2.6	17.3	3
Lemuridae	*Eulemur*	20	0.48	1.3	12.8	4
	Varecia	5	0.83	4.2	27.9	4
Lorisidae	*Nycticebus*	4	1.11	3.9	19.2	4
	Otolemur	22	1.23	5.0	22.5	4

[a]n, number of samples analyzed.
[b]1 = Dewey et al. [1994]; 2 = Oftedal & Iverson [1995]; 3 = This study; 4 = Tilden & Oftedal [1997].

when applied to diverse taxa of widely ranging body size [Oftedal, 1981, 1986]. For example, elephants do not produce low-protein milks [Oftedal & Iverson, 1995]. However, it may hold among primates. Kirkwood [1984] suggested that, when adjusted by adult weight to the three-fourths power, growth rates among primates are highest in prosimians (Kirkwood [1984] did not have data on *Eulemur* spp.), followed by New World monkeys, Old World monkeys, and finally by apes and humans. Tilden and Oftedal [1996] report growth rate data on *Eulemur fulvus* and *E. macao* that, when adjusted by adult maternal weight to the three-fourths power, are similar to the results for *Macaca* spp. reported in Kirkwood [1984]. Thus, based on growth rates adjusted by maternal metabolic size, one would predict greater proportions of energy as protein in non-*Eulemur* prosimians, followed by callitrichids and cebids, followed by *Eulemur* and cercopithicids, and finally by apes and humans. The data in Table IV yield mean protein-energy percentages of 23.2% ± 2.5%, 19.2% ± 0.8%, 12.5% ± 1.5%, and 5.9% (n = 1) for these four groups in the order predicted. Although these comparisons are based on relatively few genera, they are consistent with the growth hypothesis. Data on growth rates and milk composition from more primate genera are needed to better evaluate this hypothesis.

The variability in the *C. jacchus* and *L. rosalia* samples (Tables I and III) implies that significant interindividual variation in milk composition may be the norm among captive callitrichids. Interindividual variation in milk composition has been observed in a number of other species, including sheep [Oftedal, 1981], horses [Oftedal et al., 1983], the domestic ferret [Schoknecht et al., 1985], *Macaca fuscata* [Ota et al., 1991], and the rodents *Acomys cahirinus* and *Kerodon rupestris* [Derrickson et al., 1995]. In humans, maternal dietary intake affects the concentrations of some, but not all, milk nutrients [Lönnerdal, 1986]. The substantial interindividual variation in milk composition in *C. jacchus* and *L. rosalia* indicates that any attempt to characterize the milks of primate species from a small number of samples from a few individuals is inherently imprecise. Because the mean values presented here for the milks of *L. rosalia* and *C. pygmaea*, as well as previously published data from *Cercopithecus*, *Nycticebus*, and *Varecia* given in Table IV, represent only four to six samples per species, they should be considered approximate.

Previous reports on marmoset and tamarin milks [Jenness & Sloan, 1970; Buss, 1975; Turton et al., 1978] have been based on a small number of samples from various or unknown stages of lactation and thus cannot be considered representative. However, the reported data are within the large range we found for common marmosets (Table I).

Callitrichid females are thought to expend proportionally more energy for reproduction than most anthropoids because of the large combined mass of the twin offspring relative to maternal mass, and because many species routinely become pregnant during lactation. However, the small quantities of milk obtained from *C. jacchus* at 75 days post partum suggest that infants of this species are largely weaned from milk by this age. Infants of this age are largely self-feeding [Yamamoto, 1993]. Thus, female common marmosets likely bear the cost of lactation for only a little more than 2 months. Although common marmoset females are often pregnant during lactation, very little fetal mass is accumulated in the first 2 months [Phillips, 1976; Chambers & Hearn, 1985; Jaquish et al., 1995]. Thus, the costs of lactation and gestation appear to be temporally separated.

Callitrichids are also distinguished among anthropoids by a cooperative system of infant care that includes provisioning of infants by other members of the group during the weaning period [Garber et al., 1984; Tardif et al., 1993]. This food-sharing behavior likely reduces the infants' reliance on milk and probably reduces the energy demand on mothers. This social strategy may be a major factor that enables callitrichids to have a relatively short lactation and interbirth interval [Garber & Leigh, 1999].

Squirrel monkeys (*Saimiri* spp.) are similar in body size to callitrichids, but rear single infants over a longer lactation without supplemental provisioning of the infants by group members other than the mother, and with a longer interbirth interval. Yet the few samples of squirrel monkey milk that have been assayed appear to be similar in fat (5.1% ± 1.2%) and protein (3.5% ± 0.2%) concentrations [Buss & Cooper, 1972] to callitrichid milks. The lower sugar value (6.3%) may reflect the later lactation stage (3–5 months post partum), or may be an artifact of the reducing method used [Oftedal & Iverson, 1995]. Further research is needed to confirm this similarity, and its implication that the higher reproductive output of callitrichids relative to other anthropoids is supported by behavioral and social adaptations, rather than differences in milk composition.

It is not clear why many primates, including common and pygmy marmosets, produce milks that are dilute compared to the milks of most other mammals [Oftedal & Iverson, 1995]. There may be physiological advantages to dilute milks, especially for animals that must contend with high heat loads [Oftedal & Iverson, 1995; Tilden & Oftedal, 1997]. Evaporative cooling requires a large flux of water through the body, which in young infants must be obtained from milk. Thus high water content in milk may be important for thermal regulation in many primate infants [Tilden & Oftedal, 1997].

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