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RESEARCH ARTICLE

The Composition of Milk from Free-living Common Marmosets (*Callithrix jacchus*) in Brazil

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Common marmosets, one of the smallest anthropoid primates, have a relatively high reproductive rate, capable of producing twins or triplets twice per year. Growth and development of infants is relatively rapid, and lactation is relatively short at less than 3 months. Although mean values for the proximate composition (dry matter, protein, fat and sugar) of captive common marmoset milks fall within anthropoid norms, composition is highly variable among individual samples, with concentrations of milk fat ranging from below 1 to over 10%. To examine the extent to which this variation might be a consequence of captive conditions, we collected milk samples from wild common marmosets freely living on a farm in the state of Rio de Janeiro, Brazil. The proximate composition of the milk samples was assayed using identical techniques as used for the captive marmoset milks. The composition of the milk of wild common marmosets was also variable, but tended to be lower in dry matter, fat, protein and gross energy, and higher in sugar than milks from captive animals. Interestingly, the percentage of estimated gross energy from the protein fraction of the milks was relatively constant in both wild and captive marmosets and did not differ between wild and captive animals: 1 kcal of common marmoset milk contains on average ($\pm$SEM) $0.035\pm.001$ g of protein regardless of the gross energy content of the milk or whether the milk was from a wild or captive animal. In contrast, in 1 kcal of low-energy milks, the amount of sugar was significantly higher and the amount of fat significantly lower than in 1 kcal of high-energy milks. Thus, common marmoset milk exhibits axes of variability (especially fat concentration) as well as a significant stability in the relative amount of protein. Am. J. Primatol. 70:78–83, 2008. © 2007 Wiley-Liss, Inc.

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Lactation is a defining characteristic of mammals that is sadly understudied [Oftedal, 1984; Oftedal & Iverson, 1995]. All mammals lactate, and the diversity of the mammalian radiation is reflected in the remarkable number of lactation strategies that have evolved. The lactation strategy of a species affects the duration of lactation, the frequency of suckling, the volume of milk the mother produces per day and the composition of that milk. These parameters all work in concert to transfer nutrients from mother to infants that simultaneously satisfy infant requirements for growth and development without irreversibly compromising maternal health. Anthropoid primates in general have relatively long lactation periods, nurse their usually singleton infant frequently and produce dilute, low-energy milk. Anthropoid primates thus have evolved a lactation strategy that results in a low daily rate of transfer of maternal resources to young. This corresponds with the relatively slow growth rate and long period of dependence that generally characterizes anthropoid infants [Oftedal & Iverson, 1995].

The callitrichid primates from the New World vary somewhat from the general anthropoid pattern. They are the smallest anthropoids, ranging in body mass from a high of about 700 g in lion tamarins (*Leontopithecus* spp.) to only about 100 g in the pygmy marmoset (*Cebuella pygmaea*). Callitrichids routinely produce twins, and in captivity often triplets. Many, if not most species are capable of a fertile postpartum estrus, often resulting in multiple

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births per year. Lactation is relatively abbreviated, lasting only 2 or 3 months [Power et al., 2002]. A social structure that includes reproduction generally restricted to a single adult female per group, and a cooperative infant care system, which includes food provisioning of young by other group members, supports the rapid reduction in the infants' reliance on milk, enabling the abbreviated lactation period and shortened interbirth interval [Garber & Leigh, 1999].

Contrary to what might be predicted based on their small body size, abbreviated lactation period and increased litter size, the average composition of callitrichid milk does not seem to differ substantially from that of other anthropoids [Power et al., 2002]. The composition of milk from captive common marmosets (*Callithrix jacchus*) is the best characterized, with 41 milk samples from ten individuals over 23 lactation periods. Mean values for dry matter, fat, sugar and calculated gross energy (GE) content of milk for the common marmoset are similar to published values for Old World monkeys, although protein content is slightly higher. However, there is significant variation in composition of milks not only among females, but also among litters for the same female. Milk fat is the most variable constituent, ranging from 0.7 to 12.9% among individual samples [Power et al., 2002]. Mean values of milk constituents, however, are within anthropoid norms.

Data from captive animals must always be considered carefully when making life history and evolutionary hypotheses. Female condition is likely to affect reproduction, especially in small species such as the common marmoset that cannot store appreciable nutrient reserves. Evidence of the effect of maternal condition on lactation has been documented in the common marmoset. Small marmoset mothers rearing twins produce milks lower in energy, and their infants begin eating solid food at an earlier age [Tardif et al., 2001].

In captivity, the nutritional state of reproductive females is likely more variable than in the wild. We predict that females at either extreme of body fat are more likely to be found in the captive common marmoset population. On the one hand, marmosets may become extremely overweight in captivity owing to low activity and energy demands and high food abundance, but on the other females that are in poor condition may be able to breed in captivity but not in the wild because of food availability, lack of predation and veterinary intervention in the former situation. For example, some lactating common marmosets require medical intervention in captivity to treat such conditions as broken bones [ML Power, personal observation]; these animals would likely have died in the wild. Thus, the large variation in milk composition documented in captive common marmosets could be an artifact of captivity, and might not be representative of the lactation performance of wild animals. We hypothesized that the very high and the very low fat concentrations in milks from captive marmosets may represent females of high and low body condition in captivity, respectively, rather than be typical of milks produced by wild marmosets. To examine this issue, milk samples were obtained from feral, free-living common marmosets on a farm in the state of Rio de Janeiro, Brazil [Ruiz-Miranda et al., 2000]. These milk samples were assayed by methods identical to those employed to assay the milk samples from captive common marmosets reported in Power et al. [2002].

METHODS

A total of ten milk samples was obtained from seven common marmosets living on the Rio Vermelho farm in the state of Rio de Janeiro, Brazil: one sample each from four individuals and two samples approximately 30 days apart from three individuals. Milk samples were collected between infant ages of 2–10 weeks, similar to the times of samples from Power et al. [2002]. Captive marmoset milk samples do not systematically vary in composition over this time period [Power et al., 2002]. The ages of the infants were estimated two ways: observers followed the marmoset groups 2 days per week, and recorded the first sighting of infants. Upon capture, the ages of the infants were independently estimated based on size and physical appearance. Infant age was taken to be the mean of these two estimates. The research protocol described below was approved by the Smithsonian National Zoological Park's Institutional Animal Care and Use Committee and the appropriate Brazilian government agencies.

Animals were captured in Tomahawk live traps placed on platforms within a group's normal range. Captured animals were taken to a field laboratory where they were tattooed, so that individuals could be recognized upon recapture, weighed and examined for general health and milk samples collected from lactating females. A radio collar was placed on one animal from each group to facilitate tracking and recapture. The animals were then released in the early morning, at their capture site.

Captured lactating females were anesthetized in the field laboratory with ketamine hydrochloride (10 mg/kg body weight). Females had been separated from their infants from 4 to 6 hr before they were anesthetized, slightly longer than the 3–5 hr for captive animals [Power et al., 2002]. Once anesthetized at the field lab, the nipples were cleaned and the milk samples were collected manually by gently pressing both mammary glands. Milk was expressed into a cryovial. Efforts were made to evacuate completely both mammary glands. For each mammary, after no more milk could be expressed a final trial was attempted 1 min later. These trials at best garnered an additional drop of milk. Oxytocin was not administered. The milk samples were frozen in a −20°C freezer at Environmental Sciences Laboratory from Universidade Estadual do Norte Fluminense (UENF), in Campos dos Goytacazes—Brazil, and then shipped on dry ice to the Nutrition Laboratory of the Smithsonian National Zoological Park in Washington, DC.

Milk constituents were measured at the Nutrition Laboratory of the Smithsonian Institution National Zoological Park using standard methods [Oftedal & Iverson, 1995]. Dry matter (total solids) was measured gravimetrically after drying for 3 hr at 100°C in a forced air-drying oven. Total nitrogen (TN) was determined using a CHN elemental gas analyzer (Model 2400, Perkin-Elmer, Norwalk, CT), which provided a rapid and accurate method of assaying TN in 20 μL milk samples. In our laboratory this method has been standardized against the Kjeldahl procedure (nitrogen recovery 98–99%) and yielded comparable results for all species tested, including common marmoset milk. Crude protein (CP) was estimated as 6.38 × TN. Total lipid was measured by sequential extractions with ethanol, diethyl ether and petroleum ether by a micro modification of the Rose-Gottleib procedure. 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 from the measured constituents assuming 9.11 kcal/g for fat, 5.86 kcal/g for protein and 3.95 kcal/g for sugar. This will slightly overestimate GE because it does not account for nonprotein nitrogen [Oftedal, 1984]. Assays were performed in duplicate. Results are reported as the mean and standard error of the mean (SEM).

The relationships among the three proximate milk constituents were examined using correlation. The individual mean values for the seven wild animals were compared with the individual mean values for ten captive animal samples reported in Power et al. [2002] by multiple analysis of covariance. The amounts of sugar, fat and CP per kilocalorie of wet milk were calculated for each female in this study and for each captive female reported in Power et al. [2002]. Correlation was used to examine the variation of grams of sugar, fat and CP by the GE of the milk.

RESULTS

The wild lactating female common marmosets had a mean body mass of 382.7 ± 8.5 g. This was not different from the mean weights of high-body-weight captive lactating marmosets (381.8 ± 5.2 g) described in Tardif et al. [2001]. Upon clinical examination the lactating females were found to be in good physical condition regarding pelage, with no dental problems or other overt signs of disease. None of them showed wounds or broken bones. Milk volumes ranged from approximately 0.5 to 1.5 mL, similar to milk volumes collected from captive marmosets administered oxytocin [Power et al., 2002], implying that not administering oxytocin did not hamper complete evacuation of the mammary glands.

Milk composition varied among milk samples from the individual common marmoset females (Table I). Similar to the results for captive animals [Power et al., 2002], fat and CP in the milks of the wild females were correlated with dry matter ($r = 0.848$ and 0.902; $N = 7$; $P = 0.016$ and 0.006, respectively) and sugar was correlated negatively with milk fat ($r = -0.761$, $N = 7$, $P = 0.047$). Sugar concentration was less variable (range 7.3–8.5%) than either CP (range 1.6–3.3%) or fat (range 1.4–3.2%).

There was a 53% difference between the GE of the lowest energy milk (0.53 kcal/g) compared with the highest energy milk (0.81 kcal/g; Table I). Milk samples with higher energy contained more of the energy from fat ($r = .891$, $P = .007$), whereas milks with lower energy contained most of the energy from sugar ($r = -.983$, $P < .001$). The proportion of GE coming from CP was fairly constant at 19.8 ± 1.1% of GE ($r = .637$, $P = .124$; Table II).

TABLE I. Composition of Milk Samples for Seven Wild Common Marmosets

ID	DM (%)	CP (%)	Fat (%)	Sugar (%)	GE (kcal/g)
E1	14.4	3.3	3.2	7.3	0.77
A6	13.1 (12.7; 13.4)	2.4 (2.0; 2.7)	3.1 (2.3; 3.8)	7.5 (7.9; 7.0)	0.71 (0.64; 0.78)
M2	12.6 (13.3; 12.0)	2.1 (2.4; 1.7)	2.6 (3.8; 1.4)	8.2 (8.2; 8.2)	0.68 (0.81; 0.55)
M3	12.8	2.5	1.8	8.5	0.64
T7	13.0	2.0	2.2	8.1	0.63
O1	11.8	1.6	1.6	8.2	0.56
O2	11.4 (11.8; 11.0)	1.8 (1.7; 2.0)	1.4 (1.5; 1.3)	8.0 (8.5; 7.5)	0.55 (0.57; 0.53)
Mean (SEM)	12.7 (0.4)	2.2 (0.2)	2.3 (0.3)	8.0 (0.2)	0.65 (0.03)

For the three animals with two samples each the mean value is given, with the individuals sample values given in parentheses. Mean and SEM values for all animals were calculated using the mean values.
DM, dry matter, CP, crude protein, GE, gross energy.

TABLE II. The Percent of GE from CP, Fat and Sugar; for the Three Animals with Two Samples Each the Values for Each Sample are Given in Parentheses

ID	% GE from CP	% GE from fat	% GE from sugar
E1	25.0	37.7	37.3
A6	19.3 (18.5; 20.1)	39.1 (32.5; 44.6)	41.6 (49.0; 35.3)
M2	17.8 (17.6; 18.1)	34.7 (42.6; 22.8)	47.6 (39.9; 59.0)
M3	22.4	25.3	52.4
T7	18.3	31.2	50.5
O1	16.3	26.0	57.7
O2	19.4 (17.1; 21.7)	23.3 (23.7; 22.7)	57.3 (59.1; 55.6)
Mean (SEM)	19.8 (1.1)	31.0 (2.4)	49.2 (2.9)

Mean and SEM values for all animals were calculated using the mean values.
GE, gross energy.

TABLE III. Comparison of Milk Composition Between Seven Wild and Ten Captive Common Marmosets

	Wild animals ($n = 7$)	Captive animals ($n = 10$)	Significance (two-tailed) P
Dry matter (%)	12.7 (0.4)	13.9 (0.5)	0.077
Crude protein (%)	2.2 (0.2)	2.7 (0.1)	0.069
Fat (%)	2.3 (0.3)	3.4 (0.4)	0.051
Sugar (%)	8.0 (0.2)	7.4 (0.1)	0.008
Gross energy (kcal/g)	0.65 (0.03)	0.76 (0.04)	0.061
Percent of energy from fat	31.0 (2.4)	39.8 (2.8)	0.038
Percent of energy from sugar	49.2 (2.9)	39.3 (2.3)	0.017
Percent of energy from protein	19.8 (1.1)	20.8 (0.8)	0.461

Values are mean and (SEM) calculated from the mean values for individual animals. Values for captive marmosets are from Power et al. [2002].

In Table III, the mean values for the dry matter, CP, fat, sugar and GE of the milks of the seven wild animals were compared with data from ten captive common marmosets reported in Power et al. [2002]. The milks from this sample of free-living wild animals tended to be lower in dry matter, fat, CP and GE than that of the captive animals, whereas sugar concentration was significantly higher. A higher proportion of milk GE was derived from sugar and a lower proportion from fat in wild marmosets compared with captive marmosets (Table III). The estimated percentage of GE from protein did not differ between wild and captive animals.

Another way of expressing these relationships is to examine the amount of sugar, fat and protein per kilocalorie of milk for each of the wild ($n = 7$) and captive females ($n = 10$) by the variation in the GE of milk (Fig. 1). The grams of sugar per kilocalrie of milk were negatively associated with the GE of milk ($r = -.952$, $P < .001$), whereas the grams of fat per kilocalorie of milk were positively associated with the GE of milk ($r = .945$, $P < .001$), but there was no association between the grams of CP per kilocalrie of milk and the GE of milk ($r = .008$, $P = .975$).

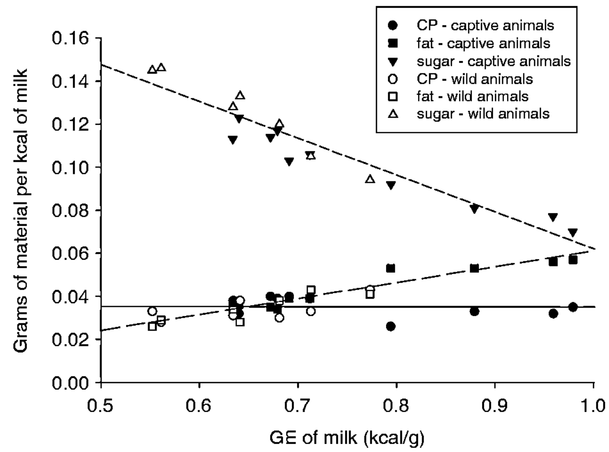

Fig. 1. The mean grams of crude protein (circles), fat (squares) and sugar (triangles) per kilocalorie of milk calculated from milk samples from individual common marmoset by the gross energy (GE; kilocalrie/gram) of the milk. Data are from ten captive animals [Power et al., 2002] and seven wild animals (this study). Data for captive animals are represented by filled symbols and for wild animals by open symbols. The regression lines (solid for CP, long dashes for fat, and short dashes for sugar) are for captive and wild data combined. Infants nursing from moms producing low-energy milk receive more grams of sugar and fewer grams of fat than do infants nursing from moms producing high-energy milk. The grams of crude protein do not depend on the GE of milk.

DISCUSSION

One of the notable findings of Power et al. [2002] is the variability in composition of common marmoset milk samples collected from captive animals maintained under identical husbandry conditions. Variability in milk composition among individuals is evident in a number of other mammals including sheep [Oftedal, 1981], horses [Oftedal et al., 1983], the domestic ferret [Schoknecht et al., 1985], the Japanese macaque *Macaca fuscata* [Ota et al., 1991] and the rodents *Acomys cahirinus* and *Kerodon rupestris* [Derrickson et al., 1995]. Milks from wild common marmosets also seemed to be variable in composition, although not to the same extent as seen in the captive animal samples. The lowest energy content milk from wild marmosets was comparable with the lowest energy content milk from captive animals; however, the highest GE from a wild marmoset milk sample was equal to the mean GE content milk of the captive animal samples. The small number of milk samples from wild animals (ten compared with 41 from captive animals) probably contributes to the lower range of variation, however, it is possible that some captive animals are able to produce higher energy milks than wild animals are able to, despite the comparable body weights of wild and captive lactating marmosets. More samples from wild animals are required to establish whether milk composition is more constrained under free-living conditions.

Despite the variability in milk composition among the wild females, the percentage of GE from CP was remarkably constant, and did not differ from that found in captive animals [Power et al., 2002]. This mirrors the findings of Power et al. [2002] that the milks of all three captive callitrichids studied (common marmosets, pygmy marmosets and golden lion tamarins) were variable in most aspects except for the percentage of GE from CP. These data from wild marmosets suggest that the consistency in the percentage of GE from CP found in captive callitrichids is not an artifact of captivity and may be a characteristic of callitrichid milk. Limited data from wild howler monkeys [Oftedal & Iverson, 1995] suggests that a percentage of GE from CP of around 20% may be typical of New World monkey milk [Power et al., 2002], although more species need to be investigated to assess this hypothesis. The percentage of GE from CP may be related to growth rates among anthropoid lineages, with New World monkeys having both the highest growth rates and the highest percentage of GE from CP [Power et al., 2002].

The possible adaptive value of a constant percentage of milk energy coming from protein is that infants that are able to satisfy their energy requirements from nursing will receive the appropriate amount of protein, regardless of variation in milk composition among females. For example, if the females in this study and the study by Power et al. [2002] were to deliver 10 kcals of milk to their infants, based on the compositional data presented the amount of milk would range from 10.2 to 18.1 g for the highest GE milk to the lowest GE milk, respectively. The amount of protein delivered to infants would average $0.35 \pm .01$ g (range 0.26–0.43 g), and would not be associated with the GE of the milk, unlike the amounts of fat and sugar (Fig. 1). Thus, the main energy substrates (sugar and fat) could vary considerably among infants based on the GE of the mother's milk, but not the amount of protein consumed. Protein intake is a constraint on the growth of lean body mass in some, but not all, nursing mammals [Oftedal, 1981].

The results from this study demonstrate the value of expressing milk composition as both percentage of mass and on a per energy basis. The value of expressing milk constituents as percentage of mass is intuitive; it is the grams of nutrient per gram of milk. Energy is a fundamental concept in science, and the transfer of energy from mother to offspring is a potentially limiting factor in reproduction. By expressing milk composition as grams of constituents per energy value of milk a clearer picture of both the gain by infants and the cost to mothers can be obtained. In this particular case, a variable constituent among milk samples from different females (the percentage of protein) was shown to be remarkably constant when expressed on a per energy basis.

A possible limitation of this study was that oxytocin was not used; thus it is possible that the mammary glands were not completely evacuated. In some species, including humans, the fat content of fore milk is significantly lower than the fat content of hind milk [Daly et al., 1993; Oftedal, 1984]. Incomplete evacuation of the mammary gland would result in an underestimate of milk fat. Considerable effort was made to express all milk that could be expressed using this protocol, and the volumes of milk obtained were consistent with expectations. Further, the change in composition between milk collected early versus late in suckling is in the fat content; appreciable differences in sugar or protein content have not been found [Attwood & Harmon, 1992]. Thus incomplete evacuation of the mammary glands would be predicted to alter the relationships between fat and the other nutrients. The consistency in the relationships among fat, sugar and protein among the milk samples from both wild animals and captive animals administered oxytocin (Fig. 1) suggests that either complete evacuation was accomplished without oxytocin, or that variation in fore and hind milk in marmosets is not significant.

These data from wild animals imply that the findings from Power et al. [2002] probably do not represent artifacts of captivity. Common marmoset milk varies in fat content and in the proportion of energy coming from fat and sugar in both wild and captive populations. The proportion of energy coming from the protein fraction of the milk varies little, however, and may represent an adaptive trait linked with infant growth rate.

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