

Effects of Reproductive Status on Energy Intake, Ingestion Rates, and Dietary Composition of Female *Cebus capucinus* at Santa Rosa, Costa Rica

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Abstract The limiting factor for fitness in female primates is the acquisition of high-quality food, i.e., food that is high in energy and nutrients, such as protein, fat, and carbohydrates. Reproductive status can influence female feeding patterns, e.g., lactating females in some primate species consume greater quantities of food and specific nutrients than do nonlactating females. We examined the energy intake, ingestion rate, and composition of the diet in female white-faced capuchins in 3 reproductive states: lactating, gestating, and cycling. We observed 12 reproductively active females for 7 mo and compared their energy intake, ingestion rates, and intake rates of nutrients: protein, fat, sugar, and fiber. Lactating females took in significantly more energy per hour while feeding than pregnant and cycling females did. Lactating females also ingested significantly more food items per hour, but they did not spend more time eating than other females did, and they did not differ in the composition of their diet as measured by insect consumption and proportion of protein. Pregnant and cycling females did not differ from each other in any of the measures. We predicted that as the infants aged and began to move independently to forage and play, their mothers' energy intake rates would decrease in concert with decreased energy demands by the infant. We found a statistically significant relationship between these 2 factors, with infant age explaining 75.4% of variation in mothers' energy intake, supporting previous studies that found lactation to be the most energetically expensive reproductive state.

Keywords *Cebus capucinus* · ingestion rate · lactation · nutrition · reproduction

Introduction

Diet is an important factor influencing a primate's fitness. Because female mammals are not generally limited by the availability of mates, a primary source of variance

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in their reproductive output is likely to be nutrition (Trivers 1972). Through the consumption of quality foods, high in available nutrients, females can increase their likelihood of producing more offspring that will survive to reproductive age. Female capuchins are highly variable in feeding and dietary patterns (Fragaszy *et al.* 2004). We examined whether female reproductive state in *Cebus capucinus* is an important factor in understanding variable feeding and nutrition patterns.

To a large extent, researchers consider lactation to be the most energetically expensive part of mammalian reproduction (Altmann 1980; Buss and Cooper 1972; Clutton-Brock *et al.* 1989; Pond 1977; Power 1999; Widdowson 1977). Researchers generally assumed that because the nursing infant is larger than the gestating fetus, lactation requires more of the mother's energy than pregnancy does (Buss and Cooper 1972). Herrera and Heymann (2004) suggested that one can expect differences in the composition of diet between lactational and nonlactational phases in females owing to the increased energy and protein requirements of lactation (Sauther and Nash 1987; Serio-Silva *et al.* 1999). Herrera and Heymann found that female titi monkeys increase the proportion of animal matter (insects) in their diet during lactation phases, as did Wright (1984). Based on the energetic demands of lactation in previous studies, we predict that lactating females will take in more energy than females in other reproductive states do. Lee (1987) noted they may accomplish this by eating longer, i.e., spending a greater proportion of their time feeding; eating faster, i.e., higher ingestion rates; eating smarter, i.e., consuming a diet that yields higher levels of protein, or all 3. We examine which of these predictions apply to the lactating females in our study group.

However, the lactational phase is not static. Lee (1987) argued that peak lactation corresponds with peak milk yield and the phase of most rapid growth of infant primates. For infant *Cebus* monkeys this phase occurs within the first few weeks of the infant's life (Fragaszy 1990a). Consequently, a capuchin mother would be expected to have increased energy intake soon after the initial postpartum period. Then, as the infant ages and becomes more independent, leaving the mother to forage and travel for brief periods, the mother's energy requirements and accordingly, energy intake rates, should decrease. This pattern occurs in lactating female vervets, in which mothers' energy intake decreases as their infants age (Lee 1987). Based on this argument, we predict that the energy intake rate of a lactating female capuchin will be higher soon after the birth of her infant and that as the infant matures and becomes more independent, the mother's energy intake rate will decrease.

Researchers consider gestation the second most expensive reproductive state (Coelho *et al.* 1977). A pregnant female should require more energy and nutrients than a cycling or anestrus noncycling female, because a portion of the nutrients ingested are transmitted to the fetus. Therefore, we predict that pregnant females will have an intermediate level of energy and ingestion rates, because they have increased costs compared to cycling females, but the growing fetus is not as demanding as the dependent infant.

Finally, we predict that cycling females will exhibit the lowest energy intake rate of the 3 reproductive states because nonpregnant, nonlactating females do not experience the additional costs of gestating or lactating for an infant. Ingestion rates, i.e., the rate at which food is consumed, should follow a similar pattern to nutrient and energy intake rates.

Methods

Study Species and Subjects

Cebus capucinus live in multimale, multifemale groups that average 17 members and exhibit female philopatry and male transfer. Researchers consider capuchins ecologically and behaviorally flexible, as evidenced in their highly variable diets and extensive range of habitat types (Fragaszy *et al.* 2004). Capuchins are classified as frugivore-insectivores, but the exact composition of their diets varies between and within groups as well as species (Chapman 1987; Fragaszy 1986, 1990b).

Between 2003 and 2004, we observed 12 adult female capuchins for 7 mo. The females were from 2 neighboring groups that Fedigan tracked for 16 and 21 yr, respectively. Each group contained 5 adult females at any 1 time during the study. At the start of our second field season, 2 females, 1 from each group, disappeared. At the same time 2 females in each group that we had previously classified as large immatures reached 6 yr, which is considered sexual maturity because females can first give birth then. Therefore, we maintained a sample size of 10 females per season, or 12 females for the entire observation period. Three females in our sample became pregnant, gave birth, or lost infants during the study period, and therefore are included in >1 reproductive category.

Study Site

We conducted the study at Santa Rosa National Park (SRNP) in northwest Costa Rica. The park is 1 section of the larger Area de Conservacion Guanacaste (ACG). It is situated near the Pan American Highway, 45 km from the border of Nicaragua and 30 km from Liberia, the capital of Guanacaste Province, with geographical coordinates 10°45' to 11°00' N and 85°30' to 85°45' W (The Government of Costa Rica 1998). SRNP consists of 10,800 ha of tropical dry forest in varying stages of succession, including evergreen, semideciduous, and recently regenerated forest. The area experiences 2 distinct seasons: a wet season from *ca.* mid-May to mid-November during which 800–2600 mm of rain falls; and a dry season from November/December until early May, during which there is virtually no precipitation (Janzen 1983).

Data Collection

We completed 7 mo of fieldwork at SRNP: 3 mo in the wet season from May through July 2003, and 4 mo in the dry season from mid-January through April 2004. In total, we included 134.6 focal h of data in the analyses. We tried to keep hours of observation equal between all subjects observed; however, because some females entered and left the group at various stages of the study period, this was not always possible.

We categorized females into 3 reproductive states based on visual observations. We used nursing behavior as the criterion to classify a female in the lactation category, though it is difficult to determine if an infant is actually obtaining milk from its mother when it suckles. We followed 8 females during their lactation periods.

We determined pregnancy via visual observation of adult females and confirmed it retrospectively after each infant was born. After *ca.* 2 mo of gestation, an adult female capuchin's abdomen becomes distended and pregnancy can be inferred. Because gestation is known to be *ca.* 5.5 mo in length (Fragaszy *et al.* 2004), one can determine the total gestation period once the infant is born. We followed 4 females during their pregnancies.

We considered cycling females to be individuals that are neither pregnant nor lactating. Though authors of preliminary research have shown that capuchin females occasionally may be nonpregnant and nonlactating, yet not cycling (Carnegie *et al.* 2005), we do not have sufficient hormonal data to determine how often and for how long this occurs. Therefore, we combined all nonpregnant/nonlactating females into the cycling female category, which comprised 5 individuals.

We examined 4 measures of the nutritional and dietary patterns of the female capuchins. The first is energy intake rate, which, expressed in kilocalories per hour, represents the calories gained from the consumption of dietary sugar, protein, and fat (and fiber in 1 of our 2 measures of energy consumption). The second measure is activity budget, which we used to estimate the relative proportion of active time devoted to feeding and foraging by females in each reproductive state. The third is ingestion rate, or the speed with which individuals consumed foods. Our fourth measure is the composition of the diet in terms of nutrient intake rate, as determined from the analysis of foods for fat, protein, sugar, moisture, and fiber. The fourth measure allows us to compare the relative importance of particular nutrients to females in each reproductive state.

Behavioral data We collected behavioral data on all the adult females via 10-min focal individual samples (Altmann 1974), via a PSION[®] Workabout hand-held computer. We recorded 7 behavioral states: feeding, foraging, resting, traveling, grooming, aggression, and other. When we observed an individual feeding, we recorded the species and number of items consumed, along with a physical description of the item ingested. We tabulated the number of food items consumed based on hand-to-mouth movements. Whenever an individual visibly picked an item from the substrate and placed the item in its mouth, we classified it as 1 item ingested. If we could not determine how many items an individual took in 1 handful, for consistency we considered 1 hand-to-mouth movement as 1 item ingested.

If an individual was out of our sight for >10% of the 10-min focal session, which occurred <10% of the time, we canceled the session and restarted once we relocated the individual (Altmann 1974). If we could not relocate the individual ≤ 10 min, we moved on to the next individual on the list. To deal with the problem of insufficient data on some individuals, we removed any individual from the analyses for which we had <15 min of feeding behavior, which resulted in the removal of 1 lactating and 1 cycling female from the analyses.

Ecological data When we observed a female feeding from a tree, we tagged the tree with flagging tape and assigned an identification number. Whenever possible, we collected a sample of the food item eaten that was similar in size and ripeness to the foods capuchins ate during the focal session. If sample collection was not possible after the focal session, we collected the sample on a day set aside for ecological data

collection (≤ 2 d later), determined the wet mass using an iBAL 201[®] Electronic Scale, then dried the sample in a food dehydrator to a constant temperature.

Cebines are very particular about the parts of a fruit they will actually swallow (Janson and Boinski 1992), and they take considerable time to separate the pulp of the fruit from the seeds or rind, which they often spit out. Therefore, we recorded which parts of the fruit, flower, or animal subjects consumed and removed the discarded portions from our samples. We stored plant samples in a dry box and insects in a freezer, until they could be transported back to Canada.

Nutritional Analyses

We took samples of food items consumed to the University of Alberta Agriculture Department Nutrition Laboratory, where we were trained on the procedures used for the nutritional analyses of fat, protein, fiber, and energy. We dried samples to a constant temperature in a drying oven at 110°C and weighed them on a LECO scale to the nearest thousandth of a gram. We determined moisture content by subtracting the final dry mass from the initial wet mass in g that had been determined in the field laboratory.

We used a LECO Nitrogen Determinator to measure the level of protein in the food samples, using the 6.25 conversion factor for nitrogen to protein (Milton and Dintzis 1981). We determined fat content after extraction with petroleum ether via the Goldfish apparatus (Sterling *et al.* 1994) to determine percent lipid composition of each sample. We determined fiber via the fiber filter bag procedure according to the methods of Goering and Van Soest (1970). We sent portions of our samples to Lab Services at the University of Guelph and to Dr. Colin Chapman (then at the University of Florida) for analysis of simple sugars via the total ethanol soluble carbohydrate method-phenol sulfuric assay using 80% ethanol solution (Danish *et al.* 2006).

We measured energy in Kcal per g via a LECO AC-300 bomb calorimeter (energy a). We corrected for the remaining fuse wire and for the number of calories produced by the formation of nitric acid. The amount of energy determined to be in each sample by the procedure may be overestimated because fiber energy is included in the result. Energy from fiber is largely unavailable to individuals without specialized digestive systems (Hladik 1981; Milton 1980). However, *Cebus capucinus* produces an enzyme, chitinase, in their digestive tract that allows them to break down chitin, the primary component of insect exoskeletons (Lambert 1998; Ullrey *et al.* 2003), which are a source of dietary fiber. Because of the uncertainty as to exactly how much energy capuchins can obtain from fiber, we also calculated available energy by summing the energy gained from the fat, protein, and sugar in the food items consumed by the monkeys (energy b).

Data Analysis

Energy intake rate We determined mean energy intake rate per h via the following formula adapted from Sterling *et al.* (1994):

$$NI = \sum_S (F \cdot X \cdot W)$$

where NI is the energy intake for 1 individual, F is the number of items consumed for 1 food species, X is the amount of energy in kcal in 1 item of the species, and W is the average mass of 1 item in g of the species. The value for all foods is summed to attain a total energy intake. We calculated an overall energy intake rate per h by dividing the total energy intake for 1 individual by the total observed feeding time in h. We took an average of females in each state to determine their mean energy intake rate per h (kcal/h).

To determine if nutrient values varied between similar species in the home range of each group, we analyzed food species from each home range separately for nutritional composition, and because we found no significant difference, we combined the data. We determined energy intake rate via 2 methods: bomb calorimeter and the summed energy gained from sugar, fat, and protein. Calorimetry measures the total energy within a food item, including fiber, which may be largely unavailable to the subject. Therefore, we compared energy intake including and excluding fiber energy. In reality, capuchins most likely gain an energy level intermediate between the 2 measures.

Activity budget We determined the time spent in each of the 7 behavioral states for each of the 3 reproductive categories of females by summing an individual's total time performing a behavior divided by the total time observed for the individual, multiplied by 100. We performed the calculation for females in each state and averaged it to determine the mean time spent feeding, foraging, resting, grooming, aggressing, traveling, or in other behaviors. We wanted to determine if females in different reproductive states spend a greater proportion of their time obtaining food and therefore combined the categories of feeding and foraging.

Ingestion rate The majority of studies addressing feeding ecology in primates have focused on the proportion of time that individuals spend feeding on different food types. However, time spent feeding may obscure differences in rate of intake for different foods in some species (Sterling *et al.* 1994). We therefore examined the overall ingestion rate of all foods consumed per h as well as the ingestion rates for animals, fruit, seeds, and flowers. We defined ingestion rate as the number of food items consumed per h of observed feeding time, as per O'Malley and Fedigan (2005).

Dietary composition: nutrient intake rate We calculated mean nutrient intake rate to compare the rate per h for each of the major nutrients measured: fat, protein, sugar, moisture, and fiber, via the same method as for energy intake rate. We calculated an overall intake rate per h for fat by dividing the total fat intake for 1 individual by the total observed feeding time in h. We took an average of females in each state to determine their mean fat intake rate, and then repeated the calculation for protein, sugar, moisture, and fiber.

Mothers' energy intake and infant age We examined the effect of infant age on lactating mothers' average energy intake rate per h, based on our prediction that a mother's energy intake would start high postpartum and then steadily decrease with increasing infant age, until it levels off at the point when the mother no longer has

excess energy requirements because of the infant. Therefore, we used a regression to examine the relationship and determine if it was significant. Our sample comprised 7 lactating females and 8 infants; 1 female lost her infant during the study and gave birth to a second infant near the end of the study period.

To control for the variability of available data on each infant, given that 4 of the infants were born at some stage during the study period and 4 were ≥ 2 mo when the study began, we used the log of the mother's average energy intake rate for the statistical analysis. We calculated the average energy intake rate per h for each mother while she was lactating and plotted it against the average age of her infant during the same interval, which resulted in an average energy intake rate for each mother based on the average age of her infant during the study. Though the method results in the loss of some detail in the data, it eliminates the variation caused by unequal data sets between individuals and results in the independence of our data points in the analysis.

Statistical Analyses

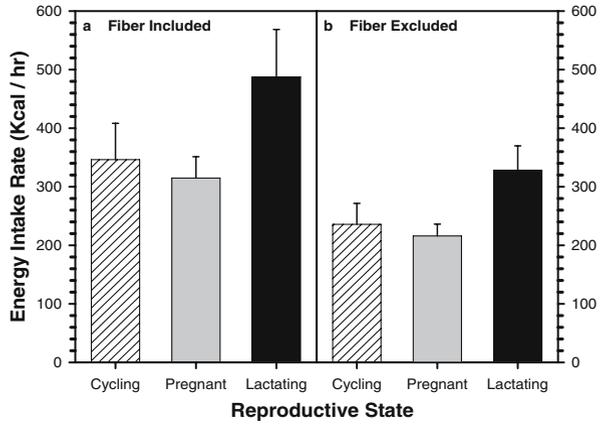
Planned comparisons We used analysis of variance (ANOVA) to test for the significance of differences among the 3 reproductive categories of cycling, pregnant and lactating females. Because the overall effect of reproductive state in the ANOVA has 2 degrees of freedom, we used planned comparisons to deconstruct the overall effect of reproductive state into 2 statistically independent and intuitively meaningful contrasts. The first contrast compared cycling females with pregnant females, while the second contrast compared lactating females with the combined group of cycling and pregnant females. We chose the 2 contrasts, because there are reasonable expectations from the literature that aspects of the diet should vary as females change from cycling to pregnancy to lactation, with the greatest differences exhibited by lactating females. In particular, we expect that females should be taking in more energy via shifts in their eating patterns as they move through pregnancy and lactation. We adjusted the tests of the contrasts when needed to account for unequal variances between groups. If the Levene statistic was significant, the values of t reported in the results were the ones adjusted for unequal variances. We applied 1-tailed tests of significance to the contrasts because there are predictions *a priori* that pregnant females should have higher rates and proportions of intake than cycling females and that lactating females should have the highest intake rates of all.

Results

Energy Intake Rates

Lactating females took in more energy per h than the combined groups of pregnant and cycling females, whether we included fiber ($t=-1.842$, d.f.=13, $p=0.044$, Fig. 1a) or excluded it from the computations ($t=-2.035$, d.f.=13, $p=0.032$, Fig. 1b). There was no tendency for pregnant females and cycling females to differ significantly in their energy intake rates whether we included fiber ($t=0.278$, d.f.=13, $p=0.607$, Fig. 1a) or excluded it from the computations ($t=0.313$, d.f.=13, $p=0.620$, Fig. 1b).

Fig. 1 Mean energy intake rate (kcal/h) for cycling, pregnant, and lactating females. We measured energy intake via 2 methods: (a) bomb calorimetry, which includes fiber and (b) summed energy from the ingestion of fat, protein, and sugar, which excludes fiber. Error bars represent 1 SEM.



Activity Budget

We examined differences in the proportion of time spent feeding and foraging for females in 3 reproductive states: lactation, pregnancy, and cycling (Fig. 2). Lactating females did not spend a greater proportion of their time engaged in feeding and foraging than the other females did ($t=0.180$, $d.f.=13$, $p=0.570$), nor did pregnant females spend a greater proportion of their time feeding and foraging than did cycling females ($t=1.584$, $d.f.=13$, $p=0.931$). In fact, the pattern, though nonsignificant, was for cycling females to spend a greater proportion of their time feeding and

Fig. 2 Feeding and foraging as a proportion of the activity budget for cycling, pregnant, and lactating females. Error bars represent 1 SEM.

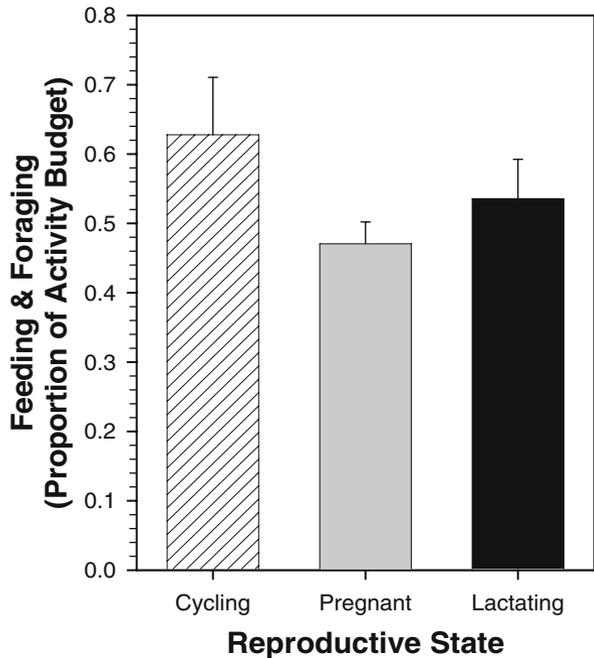
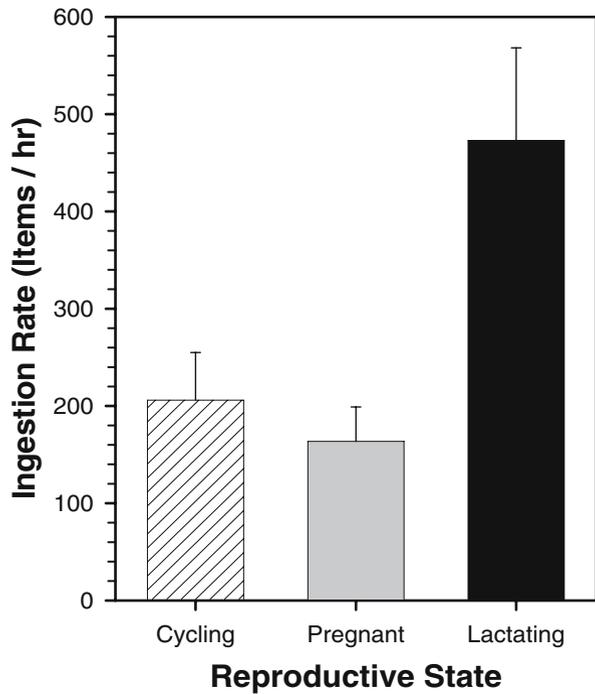


Fig. 3 Mean ingestion rates (number of items ingested/h) for cycling, pregnant, and lactating females. Error bars represent 1 SEM.



foraging than pregnant and lactating females did, which is completely contrary to the prediction.

Ingestion Rates

Ingestion rates are significantly higher for lactating females than for the combined groups of cycling and pregnant females ($t=-3.086$, d.f.=13, $p=0.004$, Fig. 3). However, there is no significant difference between pregnant and cycling females in ingestion rates ($t=0.342$, d.f.=13, $p=0.631$).

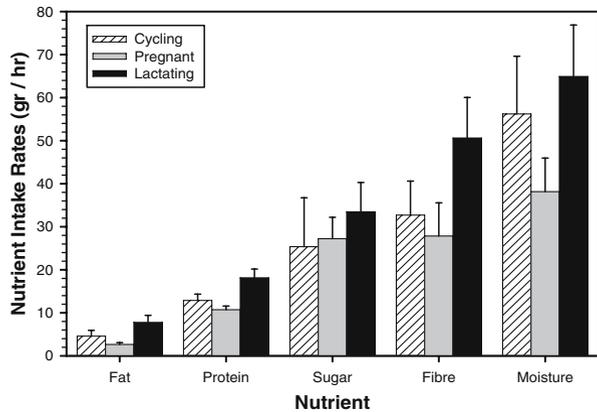
Composition of Diet

We analyzed the nutrient composition of food items consumed by the study subjects. Table I contains the average proportions of protein, fat, sugars, moisture, and fiber in the 4 major types of food items the capuchins consumed: insects, fruit, flowers, and

Table I Average nutrient composition of the major food types subjects consumed during the study

Food type	Proportion of protein	Proportion of fat	Proportion of sugar
Insects	0.636	0.150	0.014
Fruit	0.146	0.067	0.253
Flowers	0.166	0.049	0.199
Seeds	0.151	0.203	0.311

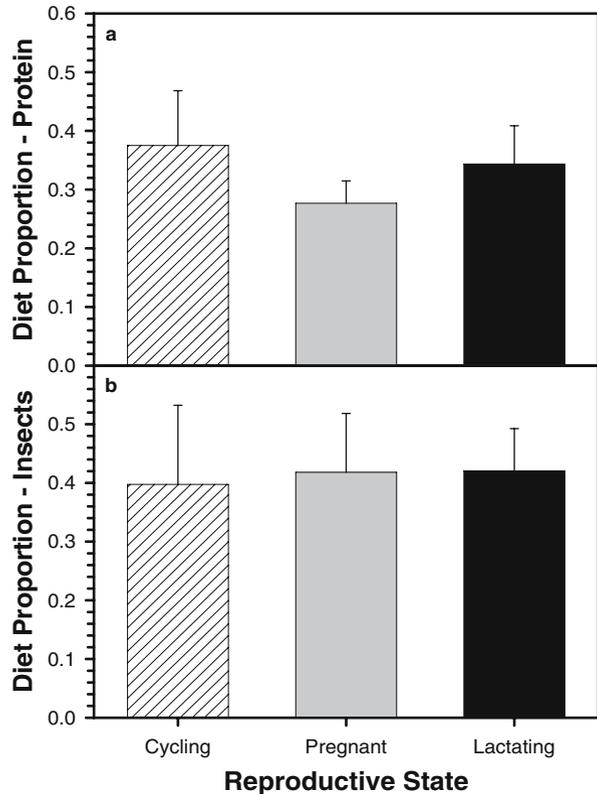
Fig. 4 Mean intake rates (g/h) of fat, protein, sugar, fiber, and moisture for cycling, pregnant, and lactating females. Error bars represent 1 SEM.



seeds. The proportion of protein in insects is >4 times the proportion of protein in fruit or seeds, confirming that insects are the food item in the capuchin diet most likely to yield high proportions of protein.

We then examined nutrient intake rates for protein, fat, sugar, moisture, and fiber by female reproductive state. Visually, there is a consistent pattern for lactating females to take in more g per h of all forms of nutrients analyzed (Fig. 4), which confirms our previous finding that lactating females take in more energy per h.

Fig. 5 (a) Protein consumption as a proportion of the total consumption of nutrients (g of protein, fat, and sugar) for cycling, pregnant, and lactating females. **(b)** Insect consumption as a proportion of the total number of food items cycling, pregnant, and lactating females ate per hour. Error bars represent 1 SEM.

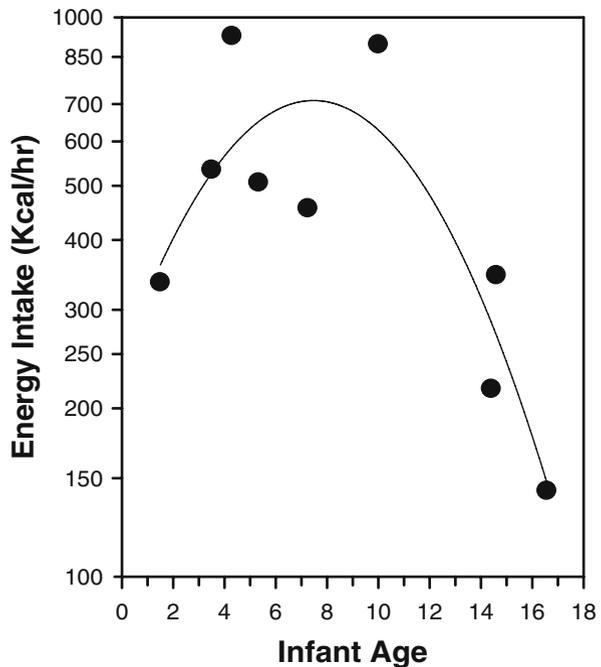


Indeed, lactating females consumed *ca.* 33% more g of protein per h than pregnant and lactating females did and twice as much fat. However, there is no obvious preference on the part of lactating females to increase their consumption of more protein any more than other forms of nutrients, e.g., sugars. That is, they did not appear to be shaping their diet differently during the lactation phase. One test of whether the dietary composition of lactating females is different from that of other females is to examine the proportion of protein in their diets. Lactating females did not make protein a greater proportion of their diets than did females in the combined groups of pregnant and cycling females ($t=0.056$, d.f.=13, $p=0.522$, Fig. 5a), and pregnant females did not have a higher proportion of protein in their diets than cycling females ($t=0.482$, d.f.=13, $p=0.681$). Finally, given the prediction from the literature that lactating females consume more insects, we tested for this specifically. Lactating females did not make insects a greater proportion of their diet than did females in the combined groups of pregnant and cycling females ($t=-0.108$ d.f.=13, $p=0.458$; Fig. 5b), and pregnant females did not consume more insects than cycling females ($t=-0.133$, d.f.=13, $p=0.448$). Females in all reproductive states consumed insects for *ca.* 40% of their diets.

Energy Intake of Lactating Females vs. Infant Age

There is considerable variation in energy intake rates for lactating females, a pattern expected if the costs of lactation vary with the age of the infant being suckled, and if energy consumption is measured for only part of the overall period of lactation. To assess whether the energy intake rates of lactating females followed a pattern of first

Fig. 6 Mothers' energy intake rates (kcal/h) as a function of the age of their infants in weeks for infants <18 wk. The line represents the second-order regression.



increasing and then declining with age of the infant, we used a second-order regression with backward elimination. One can explain 75.4% of the variation of maternal energy intake rate on the basis of infant age: $\log(\text{kcal/h})$ ($\log(Y) = 2.391 + 0.123X - 0.00825 X^2$ ($F_{2,6} = 9.2$, $p = 0.015$), and both the linear ($t = 2.436$, $p = 0.051$) and curvilinear terms ($t = -3.071$, $p = 0.022$) are significant (Fig. 6).

Discussion

Consistent with our major prediction, lactating females exhibited higher energy intake rates than pregnant and cycling females did, indicating that female white-faced capuchins fit the general argument that lactation is the most energetically expensive stage of female reproduction in mammals (Pond 1977; Widdowson 1977). Likewise Sauther and Nash (1987) found that lactating galagos consumed more food in total, and had greater energy intake rates than females in other states. However, contrary to our second prediction, pregnant females do not take in more energy than do cycling females. Our primary finding of greater energy intake by lactating females leads to the question of how greater energy intake is accomplished. Widdowson (1977) argued that lactating females have higher protein and calcium requirements than females in other reproductive states and that nursing females must either consume greater amounts of food or spend more time feeding on protein-rich foods. We examined 3 possibilities: that lactating females may eat longer than other females, or eat faster, or eat smarter (higher proportions of protein in their diet), or all 3.

Lactating females do not spend a greater proportion of their activity budget engaged in foraging and feeding than other females do and pregnant females do not spend a greater proportion of their time foraging and feeding than cycling females do, which suggests that the greater energy intake of lactating females is not accomplished via spending more of their waking hours searching for and consuming food. However, lactating females ingest food of all types at much higher rates than do other females. Indeed, ingestion rates seem to be the key to greater energy intake in lactating females. Pregnant females do not differ from cycling females in ingestion rates.

Third, we come to the prediction that lactating females may be eating a somewhat different diet than other females, specifically a diet biased to high levels of protein. Though lactating females take in more protein per h than other females do, the primary reason is that they eat insects at a faster rate than other females do, not because their diet is composed of a greater proportion of insects or protein. Indeed, unlike Herrera and Heymann (2004) and Wright's (1984) findings for red titi monkeys, we found that lactating white-faced capuchin females do not differ from other females in the proportion of insects or protein in their diets, or both. However, lactating capuchin females ingest all food types and all nutrient types at faster rates when compared to pregnant and cycling females.

Lactating primates must produce nutritious milk for their nursing infants. Nursing is critical for the survival and growth of offspring, providing not only nutrients but also maternal antibodies. The constituents of milk presumably represent a compromise between what is in the best interests of the infant and what the mother

is able to provide (Richard 1985). The energetic requirements of lactation are not constant, but vary in accordance with the changing rate of growth of the infant and thus “peak milk yield and peak metabolic demands on the mother occur in the phase of most rapid infant growth” (Lee 1987, p. 410). In our study, the mothers’ energy intake rate started high, increased during the first 8 wk of the infants’ lives and then dropped steadily until the infants reached 20 wk. A similar pattern occurred among vervets at Amboseli National Park, Kenya, where Lee (1987) compared infant age to mother’s dietary quality, measured via protein and energy levels in foods consumed. Vervet females increased their intake of high-quality foods, i.e., with high protein/energy content, steadily after the birth of their infants and maintained the increase until the infants reach *ca.* 4 mo (*ca.* 18 wk), after which their intake of high quality foods decreased.

Fragaszy (1990a) found that by 8 wk infant *Cebus* are starting to dismount and walk independently; therefore the mother now requires less energy for carrying and care. Infant *Cebus apella* gained weight rapidly during the first several weeks after birth, which may also contribute to the mother’s greater energy demands then. Milk production is not a lactating mother’s only cost. Mothers are also responsible for the constant care, thermoregulation and protection of their infants (Fragaszy 1990a). In a study of reproductive rats, Sampson and Jansen (1984) found that once the neonate is born, there is a greater demand for females to increase their energy intake, so as to provide for the adequate production of milk and thermoregulatory conditions to feed the young and ensure their survival (Serio-Silva *et al.* 1999). Each factor increases the amount of energy lactating females require. Buss and Cooper (1972) argued that the larger size of the infant as compared to the fetus increases maintenance costs for the mother. She is not only responsible for the production of nutritious milk but also must expend energy protecting, grooming, and caring for her infant.

Contrary to our prediction about the energetic costs of pregnancy, we noted no discernible difference between pregnant and cycling females in any of the measured variables. One possible explanation is that the energetic and nutritional requirements for gestation may not be as costly for capuchins as for other species, and certainly not as costly as lactation. Sauther (1994) pointed out that the costs of gestation are less than for lactation, which may explain why some species gestate instead of lactate during times of limited food availability. Indeed, Sauther and Nash (1987) argued that there may be depression of feeding during late pregnancy as compared to cycling.

In addition, costs of gestation may vary on a continuum, similar to the costs of lactation. An analysis of the energy intake rate of females during the various stages of their pregnancy might reveal differences that are concealed in our study. Because of our small sample size of 4 pregnant females, such an analysis was not feasible. However, a power analysis suggests that the lack of differences between pregnant and cycling females in our study is not entirely a matter of sample sizes. For the differences between pregnant and cycling females in energy intake to reach significance at $p=0.05$, it would take a sample size of 212 females in each of the 3 reproductive states. There was a 50% difference between energy intake in lactating vs. other females, but only a 10% difference between pregnant and cycling females. Finally, it is possible that cycling females need to maintain a high-quality diet and

high-energy intake rate similar to that of pregnant females because the cycling females are preparing for their next period of gestation.

In sum, lactating females exhibit higher energy intake rates than those of pregnant and cycling females, via faster ingestion rates instead of feeding for longer overall or switching to more protein-rich foods. Age of the infant accounts for much of the variance in energy intake rates of lactating females. Capuchins exhibit strong intragroup variability in dietary patterns, and we showed that lactation is an important factor in understanding variability in the diets of female white-faced capuchins.

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