Erratum

Effects of Individual and Group Characteristics on Feeding Behaviors in Wild *Leontopithecus rosalia*

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Kimran E. Miller^{1,2,3} and James M. Dietz¹

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Numerous errors were published due to oversights in production. We apologize for these oversights and we republish the article here in its entirety with these errors corrected.

Studies have linked variation in feeding and foraging success to variation in survival and reproductive success, which makes exploring influences on feeding invaluable. In the current study, we quantified energy contents of foods consumed by wild golden lion tamarins (Leontopithecus rosalia, GLT) and feeding behaviors of 34 GLT from March 1998 to March 1999. Our objective was to test predictions regarding effects of characteristics of the 1) individual, 2) group, 3) environment, and 4) other behaviors on 3 feeding behaviors: feeding on plant matter, searching for prey, and feeding on prey. We hypothesized that environmental characteristics, e.g., resource availability, in addition to group characteristics e.g., group size, would influence feeding on plant matter, because several individuals in a group often consume fruit in the same fruit tree. We hypothesized that environmental characteristics and individual characteristics, e.g., age, would influence searching for and consuming prey because the individual often searches for and consumes prey while it is alone at a substrate. We used SAS mixed models to determine the relative influence of these characteristics on the feeding behaviors. We found that group

¹Department of Biology, University of Maryland, College Park, Maryland 20742.

²Biology Department, Montgomery College, Rockville, Maryland 20850.

³To whom correspondence should be addressed; e-mail: bocolobo00@yahoo.com.

characteristics more significantly influenced feeding on plant matter, while individual characteristics more significantly influenced searching for prey. The results emphasize the distinctly different influences of individual and group characteristics on feeding. That influences other than competition may affect feeding on plant matter warrants further exploration.

KEY WORDS: age; competition; energy; feeding; group size; lion tamarins.

INTRODUCTION

An animal's activity budget represents a quantitative description of its response to a variety of factors influencing its survival and reproductive success (Defler, 1995). Activity budgets have been documented for many wild primate species (Altmann, 1998; Garber, 1988; Janson, 1988; Milton, 1980; Terborgh, 1983). Characteristics of the 1) individual, 2) group, 3) environment, and 4) other behaviors in the activity budget, i.e., time spent in other behaviors, may influence the amount of time an individual spends in an activity. Individual characteristics that may influence activity budgets include sex, age, weight, and physiological state (Bunnell and Gillingham, 1985; Fleming, 1988; Fragaszy, 1990). Characteristics of the group that may influence activity budgets include group size and group composition (Janson, 1988; Whitten, 1988). Environmental characteristics that may influence activity budgets include the amount of daylight, risk of predation, and resource availability (Alm *et al.*, 2002; Bunnell and Gillingham, 1985; Fleming, 1988; Fragaszy, 1990). Resource availability may vary at several levels including spatial, e.g., habitat quality, temporal, e.g., seasonal, and nutritional, e.g., energetic content. Behavioral characteristics, such as time spent in a behavior, may influence the outcome of another behavior. For example, Peres (1986) found that prey capture success was lower when golden lion tamarins (*Leontopithecus rosalia*, GLT) were involved in encounters with other groups vs. outside of encounters.

Documenting time spent feeding allows characterization of diets, identification of keystone species, determination of nutritional consumption, and observation of seasonal changes in food preferences. Exploring the relative influences on feeding lays the foundation for the creation of optimal foraging models. Components such as feeding rate, nutrient requirements, resource availability, individual expertise and group size may be identified as relevant variables influencing foraging. In addition, understanding feeding has implications for explaining several large-scale phenomena. First, food limitations can affect population demographics, dispersal, and social behavior (Koenig and Mumme, 1987; Komdeur, 1992). Dietz and Baker (1993) noted that variation in swamp habitat among territories of wild GLT was related to the number of breeding females in

the study groups, which may relate to variation in feeding. Second, food provisioning in several primate species is associated with increased birth rates and survival (Loy, 1988; Lyles and Dobson, 1988). Third, foraging success may affect birth seasonality (Di Bitetti and Janson, 2000; Goldizen *et al.*, 1988), survival, and reproductive success (Altmann, 1998).

Golden lion tamarins, endangered primates endemic to the Atlantic Coastal rainforest of Brazil (Coimbra-Filho and Mittermeier, 1973), offer an appropriate system for study of factors influencing feeding for several reasons. First, GLT have large territories relative to body size (Clutton-Brock and Harvey, 1977; Terborgh and Stern, 1987) and large variation in territory sizes among groups (territory size range: 20.2–84.1 ha, mean: 44.5 ha; Miller, 2002). Therefore, costs associated with traveling and defense may have a greater influence on feeding by GLT in large territories, as compared to those in small territories. Second, researchers have described GLT and other callitrichids as energetically constrained. Constraints may occur as a result of high litter weight to maternal weight ratios, in addition to costs associated with twinning, such as carrying, lactation, and post-weaning foraging (Dietz and Baker, 1993; Dietz *et al.*, 1994; Tardif *et al.*, 1993). The nutritional value of foods, as measured by energy content, may influence feeding behavior in GLT. For example, GLT may prefer high-energy foods and therefore spend more time consuming or searching for high-energy plant matter or prey than consuming or searching for low-energy foods. Third, an evaluation of factors affecting feeding may contribute to understanding social phenomena such as cooperative breeding, immigration, and polygyny that have been explored in other studies of wild GLT (Baker, 1991; Baker and Dietz, 1996; Bales, 2000; Dietz and Baker, 1993).

We quantified energy contents of foods consumed by GLT and tested predictions regarding effects of characteristics of the 1) individual, 2) group, 3) environment, and 4) other behaviors, i.e., time spent in other behaviors, on 3 feeding behaviors. We explored influences on the percent of time spent in the following behaviors: 1) feeding on plant matter, 2) feeding on animal prey, and 3) searching for animal prey. We chose these behaviors because they are the primary behaviors related to food intake by GLT. We did not include searching for plant matter because of difficulties associated with determining when individuals used behaviors such as visual exploration to search for plant matter. The majority of studies seeking to explain feeding behaviors test the influence of 1 or 2 of the above-mentioned characteristics and therefore present an incomplete picture of the influences on feeding (e.g., Harrison, 1985).

We made predictions describing the influence of individual characteristics, group characteristics, environmental characteristics, and time spent in other behaviors on each of the 3 feeding behaviors (Table I). We hypothesized that time spent feeding on plant matter would be primarily

Table 1. Factors potentially influencing feeding and the associated predictions describing how the factors will influence each of the 3 feeding behaviors

Factor	Independent variable	Dependent variable		
		Time eating plant matter	Time eating animal prey	Time searching for animal prey
Individual characteristics	Age	Higher for young individuals	Higher for young individuals	Higher for young individuals
	Sex	Dependent on reproductive status	Dependent on reproductive status	Dependent on reproductive status
	Body weight	Higher for heavier individuals	Higher for heavier individuals	Higher for heavier individuals
Group characteristics	Avg. monthly group size	+	+	+
Environmental characteristics	Habitat quality:			
	Average fruit kcal in territory	+	N/A	N/A
	Area of swamp in territory	+	+	+
Temporal variation in resource	Monthly availability of ripe fruits	+	N/A	N/A
	Avg. daily precipitation per month	+	+	-
	Avg. monthly day length	+	+	+

Table I. Continued

Factor	Independent variable	Dependent variable		
		Time eating plant matter	Time eating animal prey	Time searching for animal prey
Variation in nutritional value of resource	Energy content of food	+ Correlation between time spent eating specific food and energy content of food	+ Correlation between time spent eating specific food and energy content of food	+ Correlation between time spent searching for specific food and energy consumed
Behavioral characteristics (i.e., time spent in other behaviors)				
Monthly percent time in social behavior		—	—	—
Monthly percent time traveling if for purpose of finding food		+	+	+
Monthly percent time searching for prey		N/A	+	N/A
Monthly percent time eating plant matter		N/A	—	—
Avg. monthly group percent time in intergroup encounters		—	—	—

Note. A positive relationship between the dependent and independent variables is represented with a “+” symbol, while an inverse relationship is represented with a “—” symbol.

influenced by environmental characteristics, e.g., resource availability, in addition to group characteristics, e.g., group size. Like other nonsolitary primate species, multiple GLT in a group may consume fruit within the same fruit tree (Chapman, 1988a; Janson, 1988; Miller, unpublished data). We hypothesized that searching for and consuming prey would be primarily influenced by environmental characteristics, e.g., resource availability, in addition to characteristics of the individual, e.g., age. GLT, like other primates such as capuchins (*Cebus apella*, Di Bitetti and Janson, 2001), are predominantly solitary hunters. A GLT often searches for and consumes prey alone in a microhabitat, e.g., tree trunk, except in rare instances when several group members forage individually in the same very large bromeliad (personal observation; L. Rappaport, personal communication). Even in large bromeliads, group members often forage individually. Examining the relative influences of the above-mentioned characteristics on feeding allows for exploration of how evolutionary forces such as competition may affect feeding.

METHODS

Study Site and Subjects

We conducted the study from March 1998 to March 1999 in the 6300-ha Poço das Antas Biological Reserve, Rio de Janeiro State, Brazil (22° 30'–33' S, 42° 15'–19' W). Our classification of the wet and dry seasons followed that of Dietz *et al.* (1994), except that we included May and September, defined as transition months by those authors in dry and wet seasons, respectively. We defined the dry season as April–August 1998, when precipitation averaged 1.82 mm/day (SE = ± 0.74), minimum temperature averaged 17.3°C (SE = ± 1.57), and maximum temperature averaged 27.9°C (SE = ± 1.18). We defined the wet season as March 1998 and September 1998–March 1999, when precipitation averaged 7.53 mm/day (SE = ± 0.68), minimum temperature averaged 21.3°C (SE = ± 0.66), and maximum temperature averaged 31.9°C (SE = ± 0.97).

The study group included 53 wild GLT in 8 reproductive groups. We observed 18 of the 53 GLT for ≤ 2 mo and recorded < 2 h visible time for 1. We omitted data from them. The average group comprised 4.6 individuals and groups ranged from 2 to 8 GLT. Most groups contained 1 reproductive female, 1 or 2 non-natal adult males, and 1–2 litters of offspring. Most fertile copulations took place from May to July and births occurred in October and November. Reproductive females produced 1 or 2 litters per year, with 1 or 2 offspring per litter. One female produced a litter of 3 offspring during the study.

Collection of Data for Individual and Behavioral Characteristics in Table I

We observed GLT on 130 days. We defined those days in which we observed groups for 8 or more hours as full days ($n = 71$). We defined those days in which we observed groups for <8 h as partial days ($n = 59$). Data collection for partial days always began in the morning. We observed each group for an average of 1 full day ($SE = \pm 0.09$) and 1 half day ($SE = \pm 0.07$) per mo.

We defined age categories of GLT as follows (Baker, 1991; Bales, 2000; Dietz *et al.*, 1994): infants, 0–3 mo; juveniles (weaned), 3–12 mo; subadults, 12–18 mo; and adults ≥ 18 mo. We measured body masses monthly for all GLT successfully lured onto a scale in the forest (Bales *et al.*, 2002). We observed all GLT ≥ 3 mo via continuous focal animal sampling (Martin and Bateson, 1993). Each focal period collected on a randomly chosen GLT lasted for 15 min. We collected focal data on GLT throughout the partial or full day. We collected data on the following behaviors by speaking into a tape recorder: stationary, run, jump or walk, play, groom, micromanipulate (search) for prey, eat prey, eat plant matter, eat unknown matter, drink water, and fight. Micromanipulating for prey involved probing or moving substrates (leaves and bark), with the hands or mouth while looking for prey (Dietz *et al.*, 1997). We scored GLT as stationary, running, jumping or walking only when they were involved in no other concurrent behavior, e.g., groom, eat and micromanipulate. When a focal individual entered the nest site, we scored the individual as “not visible” for the rest of the focal, thus preventing an inflated score for the behavior stationary, for the last focal individual of the day.

We calculated the average monthly percent time each group spent in intergroup encounters. Encounters began when the nonfocal group was first seen or heard vocalizing and ended when the nonfocal group was no longer seen or heard. We calculated percent time spent in encounters for each group each month by dividing the total monthly time all focal individuals in a group were visible during focal periods during encounters by the total monthly time all focal individuals in a group were visible during focal periods.

Collection of Data for Environmental Characteristics in Table I

We assessed habitat quality in territories 2 ways. First, we estimated the number of kcal of fruit in each territory. We recorded geographical positions of the group (± 10 m) every 20 min and estimated territory area from 95% contour areas calculated via the Adaptive Kernel method in

ArcView (ESRI ArcView 3.1, Animal movement extension to ArcView 1.1, Hooze and Eichenlaub, 1997; $n = 8$ groups). We established transects covering 4–6% of each of the 8 territories and counted the number of plants of 24 fruit species that accounted for 70% of time spent feeding on plants during the study. To obtain measures of fruit volume, we visually estimated crown height to the nearest m for 17 species, after verifying our accuracy using a tangent height gauge. We also measured the distance from the trunk to the tree crown edge (using a tape measure), in the 4 compass directions, for 17 species. We calculated crown volume using the formula for an ellipse. We measured in the 4 compass directions, the distance from the trunk to the first fruit on the closest branch directly overhead (using a tape measure). We calculated the volume of the inner portion of the crown that did not contain fruit: nonfruit crown volume. We calculated the volume of the crown containing fruit—fruit crown volume—by subtracting the nonfruit crown volume from the crown volume. We counted fruits in 3 imaginary boxes each measuring $0.5\text{ m} \times 0.5\text{ m} \times 0.5\text{ m}$, in 2–3 trees for each species. We estimated the number of boxes that would fit in the fruit crown volume and calculated the average number of fruits in the fruit crown for each species (Miller and Dietz, 2004).

To estimate the total number of kcal of food from each species in 1 ha, we multiplied the number of kcal/g of dry fruit for a species by the average number of g of dry fruit/tree for that species by the average number of trees of that species/ha. We multiplied the sum of kcal from all species per ha by territory area to obtain estimates of the total number of kcal/territory. We explain the methodology used to obtain kcal content and mass of dry fruit matter below. We focused on species with the exception of *Musa* sp. and Myrtaceae sp. 3 (Table II) on which GLT spent >1% of their feeding time. Thus, our measures of territory kcal are the result of data from 11 species, which accounted for 62% of time spent feeding on plants.

We calculated a second measure of territory quality by estimating the area of swamp in each territory. We counted trees with fruits edible to GLT in 10 transects each measuring $50\text{ m} \times 10\text{ m}$ and found that swamp forest had 564 fruit trees/0.5 ha, while hillside forest had 131 fruit trees/0.5 ha. Because of the high density of fruits in swamp habitat, the area of swamp in a territory may serve as a relevant measure of habitat quality (Dietz and Baker, 1993). We calculated the area of swamp in each territory in the same way as for territory size.

We assessed monthly availability of ripe fruits by collecting phenological data from 3 parallel, 10-m-wide transects in 2 contiguous GLT territories. Transects covered an area of $17,500\text{ m}^2$. We assessed fruit phenology for 17 species commonly eaten by GLT (93 plants). We observed ≥ 5 plants of each species along the transects except for *Ficus* sp. ($n = 3$ trees), which was relatively rare. We assigned ranks that described a plant's phenological stage

Table II. Percent time spent feeding on fruits, nectar and exudates that could be identified (March 1998–March 1999)

Scientific name or common name	Percent time feeding	Caloric value (kcal/g dry matter)
<i>Cecropia hololeuca</i>	11	5.097 ^a S
<i>Symphonia globulifera</i> (nectar)	11	—
<i>Miconia</i> sp. 2	9	4.881 ^a S
<i>Miconia cinnamomifolia</i>	7	4.871 ^a S
<i>Henriettea saldanhei</i>	6	4.013 ^a S
<i>Miconia prasina</i>	6	3.986 ^a S
<i>Euterpe edulis</i>	5	3.987
<i>Ficus clusiifolia</i> or <i>obtusiuscula</i>	5	4.966 ^a S
<i>Eugenia moraviana</i>	4	4.028
<i>Myrcia racemosa</i>	4	5.372
Unknown fruit sp. 1	4	4.165
<i>Cordia sellowiana</i> or <i>taguayensis</i>	3	3.842
<i>Musa</i> sp. 1	3	3.986
Myrtaceae sp. 3	3	4.068
<i>Symphonia globulifera</i> (fruit)	2	4.375
<i>Anacardium occidentale</i> (exudate), <i>Mimosa bimucronata</i> (exudate)	1	4.127
<i>Eugenia</i> cf. <i>cappariifolia</i>	1	4.052 ^a SK
<i>Monstera</i> sp.1	1	3.707
<i>Genipa americana</i>	1	3.963
<i>Lacistema pubescens</i>	1	—
<i>Plinia</i> sp. 1	1	3.940
<i>Myrcia anceps</i>	0.9	4.947
<i>Bactris setosa</i>	0.8	3.877
<i>Psidium guaiava</i>	0.7	3.683
Unknown fruit sp. 3	0.7	—
<i>Miconia albicans</i>	0.6	4.270 ^a S
<i>Miconia</i> sp. 1	0.6	4.285 ^a S
<i>Asplundia brachypu</i> or <i>Thoracocarpus bissectus</i>	0.5	5.839 ^a S
<i>Ficus</i> sp. 1	0.4	4.728 ^a S
<i>Inga thibaudiana</i> , <i>affinis</i> , <i>cordistipula</i> or <i>lepantha</i>	0.4, 0.4	4.410, 4.274
<i>Miconia staminea</i>	0.4	4.292 ^a S
<i>Tournefortia breviflora</i>	0.4	—
<i>Tovomitopsis paniculata</i>	0.4	4.129
Unknown fruit sp. 2	0.4	4.633
Unknown fruit sp. 4	0.4	4.335
<i>Cecropia glaziovii</i> or <i>lyratiloba</i>	0.3	4.535 ^a S
<i>Elaeis guineensis</i>	0.3	7.333
Urticaceae sp. 1	0.3	—
<i>Syzygium jambos</i> (fruit)	0.3	3.926
Myrtaceae sp. 5	0.2	4.023
Unknown bromeliad sp. 1	0.2	3.720
<i>Monstera</i> sp. 2	0.1	3.714
<i>Faramea multiflora</i> var. <i>salicifolia</i>	0.1	3.913
<i>Hirtela</i> sp. 1	0.1	—
<i>Marlierea</i> cf. <i>glazioviana</i>	0.1	—
Myrtaceae sp. 1	0.1	—
Myrtaceae sp. 2	0.1	4.433

Table II. Continued

Scientific name or common name	Percent time feeding	Caloric value (kcal/g dry matter)
Myrtaceae sp. 4	0.1	4.244
<i>Pradosia latescens</i>	0.1	4.572
<i>Tapirira guianensis</i>	0.1	—
Unknown fruit sp. 5	0.1	4.775 ^a S

Note. Time spent feeding on these species represents 94% of all time spent feeding on plant matter. Caloric values are also given for the fruits and exudates.

^aThese energy values are of plant matter that included parts not eaten and/or digested by GLT (SK = skin, S = seed).

monthly from May 1998 to May 1999 and included the following: 0—no fruits or flowers present or flowers or unripe fruits present; 1—few ripe fruits, but mostly unripe fruits present; 2—approximately half of fruits are ripe and other half of fruits are unripe; 3—more ripe fruits than unripe fruits present; 4—only ripe fruits present; 2.5—few ripe fruits present (more fruits than category 2, but fewer than categories 3 and 4) and fruiting period ending. Of the 17 species, we focused on the 13 species on which GLT spent $\geq 1\%$ of their feeding time. We summed the highest ranks for all species that fruited in a month for each month to estimate monthly fruit availability.

We recorded precipitation and temperature daily at Poço das Antas Reserve. The onset of flowering and fruiting is often the result of precipitation that occurred weeks or months before (Chapman, 1988b). Because of the lag time between rainfall and its effects on plant phenology, we used measures of precipitation recorded 1 mo and 2 mo prior to observations of feeding on plant matter to test the effects of precipitation on percent time feeding on plant matter.

Insect availability is also related to precipitation in the tropics (Buskirk and Buskirk, 1976; Janzen, 1973). Therefore, we used measures of precipitation recorded 1 mo prior to observations of feeding on prey or searching for prey to test the effects of precipitation on percent time feeding on prey and searching for prey. We collected insect wings, which were never eaten by the GLT to aid in prey identification (July 1998 to March 1999). We calculated average monthly day lengths via a website created by the U.S. Naval Observatory, Astronomical Observation Department, Washington, D.C. (<http://www.mach.usno.navy.mil/AA/data>).

We measured the energy content of foods eaten by GLT as an estimate of the nutritional value of the foods consumed. We collected fruits from all but 9 species that GLT fed on for ≥ 1 min and exudates (gum and sap) from trees and vines where GLT fed (Table II). At the Centro de Ciências e Tecnologias Agropecuárias, Universidade Estadual do Norte Fluminense (Campos, R.J. State, Brazil), we separated fruits into seed, skin, and pulp

for the purpose of separating parts eaten from parts not eaten by GLT. We weighed the samples and dried them at 60°C until repeated measures of weights ceased to change. We divided the mass of the dry matter in a sample by the number of fruits originally collected to obtain the mass of dry matter of the fruit part(s) eaten by GLT/fruit.

We ground all samples into powder and redried them at the Human Nutrition Research Center, USDA (Beltsville, Maryland). We determined the energy values of the exudates and fruit parts eaten by GLT via a 1261 Parr Isoperibol calorimeter (Parr Instrument Company, Moline, IL). We ran 2 trials with benzoic acid daily to ensure that the calorimeter was consistent among days. We calculated final caloric values by subtracting the number of kcal created when the fuse wire burned and when nitric acid was formed from calorimetric readings. We had sufficient plant material to run duplicate trials for all but 7 fruit species to test for consistency between trials. We tested for a correlation between energy content/g of dry matter and percent time spent feeding on plant matter for all species on which GLT spent $\geq 1\%$ of their feeding time ($n = 18$ species).

Statistical Analyses

We used SAS Proc Mixed to test mixed models—similar to regression models—that explained percent time spent feeding on plant matter, feeding on prey, and searching for prey (SAS Institute, Inc. 1999). Mixed models are appropriate for analyses that involve variables that are randomly assigned, e.g., individual ID, and variables that are not randomly assigned, e.g., temperature (Diggle *et al.*, 1994).

The time of day may influence the percent time an individual spends in a behavior, in which case, our behavioral data would vary among partial and full days. Therefore, we examined the influence of time of day on percent time spent in behaviors. We divided full days into morning periods (6:00–11:59 h) and afternoon periods (12:00–18:00 h) and grouped behaviors into categories: stationary, travel (walk and run), eat plant matter, eat prey, and search for prey. We used a mixed model to test the influence of time of day on percent time spent in each of the above-mentioned 5 behaviors. We included time of day as a fixed effect and date and group ID as random effects in the 5 models predicting time spent in a behavior. We also included percent time spent in encounters (as a fixed effect) in the models because encounters occur primarily in the morning (Miller, unpublished data) and may differentially affect time spent in a behavior during partial and full days.

In the 3 models predicting percent time spent consuming plant matter, searching for prey, and consuming prey, we include the variables group

ID and GLT ID as random effects, while all other variables were fixed effects. We transformed the data via an arcsin square root transformation for percent time spent consuming plant matter and percent time spent consuming prey, and a log transformation for percent time spent searching for prey.

We removed nonsignificant variables from each model via backward selection, which determined the relative influence of each independent variable in the model. The independent variables for each of the 3 feeding models are listed in Table I. The resulting graphs illustrate the relative influence of a single variable on feeding, unless they depict an interaction between 2 variables. We tested for multicollinearity by examining the condition index and tolerance. All condition indexes were <10 and all tolerance values were >0.05 . Therefore, we assumed correlation between the independent variables, e.g., percent times spent in activities in the model did not influence the results. We used the Spearman correlation coefficient to test for a relationship between energy contents of plant species and percent time spent consuming plant species.

RESULTS

Interobserver reliability between the primary author and assistant averaged 96.5%. Therefore, we pooled behavioral data collected by both observers. Time of day was not a significant predictor of percent of time eating plant matter or prey, traveling, remaining stationary, or searching for prey. As a result, we pooled behavioral data collected during partial and full days for each GLT each month. The sampling unit for behavioral data was time spent in a behavior/time visible per GLT per mo. We observed GLT for 373.4 visible hours. We observed each GLT for an average of 1.2 visible h/mo ($SE = \pm 0.1$), with a minimum of 0.7 visible h/mo.

Figure 1 shows the average activity budget of the study subjects. Average monthly percent times spent in activities included the following: 3% eating prey, 7% searching for prey, 8% traveling, 13% eating plant matter, and 66% stationary. Traveling included walking/jumping, which averaged 0.79 m/s ($SE = \pm 0.08$). We omitted time spent running, which averaged 1.8 m/s ($SE = \pm 0.27$), from the graph because GLT spent $<1\%$ of their monthly time in the activity. We also omitted time spent playing and grooming because GLT spent an average of 1% of their time in each of these behaviors. Groups spent an average of 17% of their time involved in encounters with conspecifics ($SE = \pm 3\%$). Table III shows the average activity budget and group size for each of the 8 groups.

Fig. 1. Activity budgets of 34 GLT in 8 groups, March 1998–March 1999 (373.4 visible hours). We omitted behaviors including fighting, drinking water, eating unknown matter, and running from the graph because GLT spent <1% of their time in these activities. We also omitted playing and grooming because the average percent times spent in these activities were 1%. Behaviors in the graph’s legend are listed in the same vertical order as the sections in each bar.

Percentage Time Spent Feeding on Plant Matter

We identified 54 plant species eaten by GLT, which accounted for 94% of the total time spent feeding on plant matter (Table II and IV). The

Table III. Average group activity budgets for 8 study groups, March 1998–March 1999 (373.4 visible hours)

Group	Size	Average percent time spent in activity				
		Eat prey	Search for prey	Eat plants	Stationary	Travel
2F	5.3	4	10	17	61	11
2M	5.1	5	9	23	54	11
BA	2.9	4	6	8	73	8
BO	3.3	3	7	11	71	7
FA	4.6	5	7	16	64	11
GF	5.9	5	10	19	62	10
PP	3.3	4	9	15	61	10
SA	6.6	4	12	21	62	11
Average of “small groups” (Average group size of 3: BA, BO, PP)		4	7	11	69	8
Average of “large groups” (Average group size of 6: 2F, 2M, FA, GF, SA)		5	9	19	61	11

Note. We omitted behaviors including fighting, drinking water, eating unknown matter, and running from the table because GLT spent <1% of their time in these activities. We also omitted playing and grooming because the average percent times spent in these activities were 1%. Average group sizes for the 8 groups are also included. Average percent times spent in each activity are also given for “small” and “large” groups.

remaining 6% was spent feeding on unidentified plant matter. Of the time spent feeding on identified plant matter, 88.3% was spent on fruits, 10.4% on nectar from *Symphonia globulifera* flowers, and 1.3% on exudates. GLT consumed fruit from 49 species of trees and 3 species of bromeliads, flower nectar from 2 of the fruit species (primarily *Symphonia globulifera*, once from *Syzygium jambos*), and exudates from 2 identified species (*Mimosa bimucronata*, *Anacardium occidentale*) and other unidentified species. GLT spent between 0.1% and 11% of feeding time consuming plant matter from each species. GLT spent $\geq 1\%$ of their feeding time consuming plant matter from each of 21 species (Table II). Time spent feeding on these 21 species accounted for 89% of the total time spent feeding on plant matter that could be identified.

Table V includes a list of variables tested in the model to explain monthly percent time feeding on fruits (identified, unidentified), flower nectar, and exudates. The significant variables predicted 37% of the variation in percent time feeding on plants ($r^2 = 0.37$). The group characteristic, group size, most strongly affected percent time feeding on plant matter and explained 16% of the variation ($r^2 = 0.16$). As predicted, GLT in large groups spent more time eating plant matter than those in small groups (Figure 2).

Percent time traveling had the second strongest influence on percent time feeding on plants, explaining 6% of the variation in percent time feeding on plants. GLT that spent more time traveling also spent more time eating plants. Because GLT in large groups spent more time eating plants, we explored the possibility of a similar relationship between group size and traveling. Time spent traveling was not correlated with group size (Spearman correlation, $r_s = 0.65$, $p = 0.10$). There was also no correlation between group size and territory size (Spearman correlation $r_s = 0.66$, $p = 0.08$) or between group size and group average percent time spent in intergroup encounters (Spearman correlation $r_s = 0.37$, $p = 0.36$).

We developed a series of hypotheses and predictions post hoc to explore further the relationship between group size and percent time spent consuming plants. With these hypotheses, we also investigated the extent to which competition may influence GLT feeding behavior (Table VI). Individuals in large groups may spend more time eating plant matter than those in small groups for 3 reasons: 1) An advantage to greater time spent eating, e.g., increased body mass, is associated with increased reproductive success and individuals in large groups have the greatest access to food resources and are able to spend more time feeding than small groups can. 2) The same advantage exists, but there is no variation in resource availability. Instead, individuals in large groups have some characteristic related to feeding success, e.g., experience or cognitive map, that allows them to spend more time feeding than small groups, and 3) Individuals

Table IV. Plant species eaten by GLT with month when eaten and part of plant consumed and digested, March 1998–March 1999

Family	Fruit species	Month(s) eaten	Part(s) eaten
Anacardiaceae	sp. 1	September	P, SK
Anacardiaceae	<i>Tapirira guianensis</i>	January–February	P, SK?
Anacardiaceae ^b	<i>Anacardium occidentale</i>	June, August	EX
Araceae	<i>Monstera</i> sp. 1	February–March, June–September	P, SK
Araceae	<i>Monstera</i> sp. 2	March	P, SK
Arecaceae	<i>Bactris setosa</i>	June–October	P
Arecaceae	<i>Euterpe edulis</i>	May–August	P when unripe
Arecaceae ^b	<i>Elaeis guineensis</i>	August–September	P, SK?
Boraginaceae	<i>Cordia sellowiana</i> or <i>taguayensis</i>	February–March, June–September	P
Boraginaceae ^a	<i>Tournefortia breviflora</i>	November	P, SK
Chrysobalanaceae ^a	<i>Hirtella</i> sp. 1	October	P, SK
Clusiaceae	<i>Symphonia globulifera</i>	N: March–May, December; P: October–January	P, N
Clusiaceae	<i>Tovomitopsis paniculata</i>	August–November	P
Cyclanthaceae	<i>Asplundia brachypu</i> or <i>Thoracocarpus bisectus</i>	August–September	P
Lacistemaceae ^a	<i>Lacistema pubescens</i>	October–November	P, SK
Leguminosae–Mimosoidae ^a	<i>Mimosa bimucronata</i>	April, July–August	EX
Leguminosae	<i>Inga thibaudiana</i> , <i>affinis</i> , <i>cordistipula</i> or <i>letpantha</i>	January, March, July–September, November	P
Melastomataceae	<i>Henriettea saldanhei</i>	February–March, June–December	P
Melastomataceae	<i>Miconia albicans</i>	October–November	P, SK
Melastomataceae	<i>Miconia cinnamomifolia</i>	January–March, May	P, SK
Melastomataceae	<i>Miconia prasina</i>	February–March, June–December	P, SK

Table IV. Continued

Family	Fruit species	Month(s) eaten	Part(s) eaten
Melastomataceae ^a	<i>Miconia</i> sp. 1	August	P, SK
Melastomataceae	<i>Miconia</i> sp. 2	June–September	P, SK
Melastomataceae ^a	<i>Miconia staminea</i>	June, August	P, SK
Musaceae	<i>Musa</i> sp. 1	Months provisioned	P
Myrtaceae	<i>Eugenia moraviana</i>	February– March, October– November	P, SK
Myrtaceae	<i>Myrcia anceps</i>	May–June, October	P, SK
Myrtaceae	sp. 1	February–March	P, SK?
Myrtaceae	sp. 2	January	P
Myrtaceae	sp. 3	July–September	P, SK
Myrtaceae	sp. 4	October	P, SK
Myrtaceae	sp. 5	August	P
Myrtaceae ^a	<i>Eugenia</i> cf. <i>capparidifolia</i>	June–August	P
Myrtaceae ^a	<i>Marlierea</i> cf. <i>glazioviana</i>	September– October	P, SK
Myrtaceae ^a	<i>Myrcia racemosa</i>	August, October– December	P, SK
Myrtaceae ^a	<i>Plinia</i> sp. 1	July–September	P, SK
Myrtaceae ^a	<i>Psidium guaiava</i>	February–March	P
Myrtaceae ^a	<i>Syzygium jambos</i>	P: November, December; N: August	P, SK sometimes, N
Rubiaceae	<i>Tocoyena bullata</i> ^b	July	P, SK?
Rubiaceae ^a	<i>Faramea multiflora</i> var. <i>salicifolia</i>	March, December	P, SK
Rubiaceae ^a	<i>Genipa americana</i>	June–July	P
Sapotaceae ^a	<i>Pradosia latescens</i>	June	P, SK
Unknown	Bromeliad sp. 1	September	P, SK
Unknown	Fruit sp. 1	October– December	P, SK sometimes
Unknown	Fruit sp. 2	July–August	P, SK sometimes
Unknown	Fruit sp. 3	October	P, SK sometimes
Unknown	Fruit sp. 4	August	P
Unknown	Fruit sp. 5	March	P, SK
Unknown	Vine sp. 1	November	vine
Urticaceae	<i>Cecropia hololeuca</i>	March– November	P, SK
Urticaceae	<i>Ficus clusiifolia</i> or <i>obtusiuscula</i>	January–March, June, August– October	P, SK
Urticaceae	<i>Ficus</i> sp. 1	August, December	P, SK?

Table IV. Continued

Family	Fruit species	Month(s) eaten	Part(s) eaten
Urticaceae	sp. 1	December	P, SK?
Urticaceae	<i>Cecropia</i> <i>glaziovii</i> or <i>lyratiloba</i>	January— March, October, December	P, SK

Note. Parts eaten: P = fruit pulp, SK = fruit skin, S = fruit seed, N = nectar, EX = exudates.

^aIdentified by João Marcelo Alvarenga Braga and Marcelo Trindade Nascimento LCA/CBB/UENF.

^bIdentified using Heywood (1993). All others were identified by Jardim Botânico, Poço das Antas Reserve.

in large groups spend more time feeding than those in small groups for the purpose of compensating for the negative effects of feeding competition (Table VI). We tested the first and third hypotheses. Relative to the first hypothesis, there was no relationship between group size and territory quality (Table VI). Relative to the third hypothesis, there was no significant difference in the average DBH (diameter at breast height) of fruit trees fed from (for the 7 important fruit species) by small vs. large groups (Table VI). There was also no significant difference in the average sum of fruit trees (for the 7 fruit species) fed from/h visible by small vs. large groups (Table VI). In addition, there was no significant difference in average consumption duration/whole fruit (for the 7 fruit species), for small vs. large groups (Table VI).

Age, percent time spent in social behaviors, precipitation, and day length significantly influenced monthly percent time eating plants, but to a lesser degree than group size and time spent traveling. Juveniles/subadults generally spent more time eating plant matter than adults did (average percent time $\pm$ SE: adult = 15% $\pm$ 0.01; subadult/juvenile = 22% $\pm$ 0.02). There was a significant effect of the interaction between age and group size on percent time eating plant matter, such that there was a trend for juveniles/subadults to spend more time eating plant matter than adults did, as group size increased (Fig. 3). As predicted, percent time spent in social behaviors—play, groom—showed an inverse relationship with percent time eating plants. Also, average daily precipitation/mo with a 2-mo lag had a positive relationship with percent time eating plants. Feeding during months that had heavy rainfall 2 mo before was greater than feeding during months with less rainfall 2 mo before. Contrary to what was predicted, average monthly day length showed an inverse relationship with percent time eating plants. During months of short day lengths, GLT spent a higher percent time consuming plant matter.

Table V. Variables tested in the 3 mixed models associated with feeding behavior

Independent variable	Model I Eat plant matter	Model II Eat animal prey	Model III Search for prey
Individual characteristics			
Age	$p < 0.05, F_{1,219} = 3.89$	NS	$p < 0.0001, F_{1,171} = 18.53$
Sex	NS	NS	NS
Body weight	NS	NS	NS
Group characteristics			
Avg. monthly group size	$p < 0.0001, F_{1,219} = 22.30$	NS	NS
Interaction between age and group size	$p < 0.01, F_{1,219} = 6.36$	NS	NS
Environmental characteristics			
Habitat quality			
Avg. fruit kcal in territory	NS	—	—
Area of swamp in territory	NS	NS	NS
Monthly availability of ripe fruits	NS	—	—
Avg. daily precipitation per month (1-mo lag)	NS	NS	NS
Avg. daily precipitation per month (2-mo lag)	$p < 0.001, F_{1,219} = 11.66$	—	—
Avg. monthly day length	$p < 0.0001, F_{1,219} = 22.83$	NS	$p < 0.05, F_{1,171} = 4.26$
Behaviors			
Monthly percent time in social behavior	$p < 0.0005, F_{1,219} = 14.17$	$p < 0.05, F_{1,171} = 5.86$	NS
Monthly percent time traveling	$p < 0.0001, F_{1,219} = 21.71$	NS	$p < 0.0001, F_{1,171} = 16.76$
Monthly percent time searching for prey	—	$p < 0.005, F_{1,171} = 9.00$	—
Monthly percent time eating plant matter	—	NS	NS
Avg. monthly group percent time in encounters	NS	$p < 0.05, F_{1,171} = 4.09$	NS
Model r^2 value	0.37	0.08	0.25

Note. — = variable not tested in model; NS = variable not significant in model. Those variables found to be significant predictors in the models have p values and F values given for them. No variables associated with plant availability were included in the models associated with animal prey. If the relationship between the independent and dependent variables was in the direction predicted in Table I, the significant statistics are underlined in each model.

Fig. 2. Average group size and average group member's percent time eating plant matter. In the mixed model, group size significantly influenced time spent eating plant matter, such that GLT in larger groups spent more time consuming plant matter than those in small groups ($p < 0.0001$, $F_{1,219} = 22.30$).

Table VI. Post hoc hypotheses, predictions, methodology, and statistics addressing the relationship between group size and time spent feeding on plants. These hypotheses investigate the extent to which competition may influence feeding behavior of GLT

Observed result: Individuals in large groups spent more time consuming plants than individuals in small groups.

Individuals in large groups may spend more time eating plant matter than those in small groups for 3 hypothesized reasons. We tested H1 and H3 only.

H1: An advantage to greater time spent eating exists (e.g., increased body weight is associated with increased reproductive success) and those individuals in large groups have the greatest access to food resources and are able to spend more time feeding than small groups.

P1: Group size should positively correlate with territory quality. Territory quality may be measured at several levels: 1) temporal—seasonal fruit availability, and 2) spatial—habitat availability; availability of fruit kcal in the territory.

Statistics: Spearman correlation:

Group size and average monthly availability of ripe fruits ($r_s = -0.59$, $p = 0.13$)

Group size and area of swamp habitat in the territory ($r_s = 0.14$, $p = 0.75$)

Group size and average fruit kcal in the territory ($r_s = 0.44$, $p = 0.27$)

H2: The same advantage exists (as stated in the above hypothesis), but there is no variation in resource availability. Instead individuals in large groups have some characteristic related to feeding success (e.g., experience or cognitive map) that allows them to spend more time feeding than small groups.

P1: There is no positive correlation between group size and territory quality.

P2: There is a positive relationship between group size and characteristics of the individual, such as feeding experience (e.g., receiving food shares) or cognitive mapping ability.

H3: Individuals in large groups spend more time feeding than those in small groups for the purpose of compensating for the negative effects of feeding competition.

P1: The rate of agonism in fruit trees will be higher for large groups than for small groups.

P2: Large groups will feed from larger fruit trees/day than small groups.

P3: Large groups will feed from more fruit trees/day than small groups.

P4: Large groups will have shorter ingestion rates in fruit trees than small groups.

Table VI. Continued

Brief methodology for H3 and resulting statistics:

P1: Not tested owing to lack of consistent data.

P2: We recorded the circumferences of all trees from which focal GLT fed during March 1998–March 1999. We summed the circumferences of all trunks for those trees that had more than 1 trunk. We converted the circumferences into DBH measurements (diameter at breast height). We tested this prediction using the 8 fruit species from which GLT spent 5% or more of their feeding time (Table II). We calculated an average daily DBH for each of the 8 fruit species for each of the 8 groups. If a tree was visited twice, its DBH was counted twice. We then calculated an average DBH for each of the 8 fruit species for small groups (average group size of 3: BA, BO, PP; Table III) and an average DBH for each of the 8 fruit species for large groups (average group size 6: 2F, 2M, FA, GF, SA; see Table III). We omitted 1 fruit species in the comparison because the 3 small groups never fed at the species (*Miconia cinnamomifolia*). We used a Wilcoxon signed-rank test to compare the average DBH values of the 7 fruit species fed from, for small vs. large groups.

Statistics: Average DBHs of fruit trees of 7 species fed from by “small” vs. “large” groups:

average DBH_{small group} = 15.3 (SE = ± 3.7), average DBH_{large group} = 19.0 (SE = ± 5.4); $p = 0.58$, $W = -8.0$, 7 pairs.

P3: We summed the number of fruit trees of each of the 8 fruit species (as mentioned in P2) that each group (all focal GLT) fed from daily, during March 1998–March 1999. We then divided these sums for each group by the total time each group was visible during observations (sum of trees fed from/h visible). We then calculated an average sum of fruit trees fed from/h visible for “small groups” (average group size of 3: BA, BO, PP; Table III) and an average sum of fruit trees fed from/h visible for “large groups” (average group size 6: 2F, 2M, FA, GF, SA; Table III), for each of the 8 fruit species from which GLT fed. Once again, we omitted 1 fruit species in the comparison because the 3 small groups never fed at the species (*Miconia cinnamomifolia*). We used a Wilcoxon signed-rank test to compare the average sums of trees of the 7 fruit species fed from/h visible, for “small” vs. “large” groups.

Statistics: Average sum of fruit trees of 7 species fed from/h visible by “small” vs. “large” groups: average Sum/h visible_{small group} = 0.31 (SE = ± 0.11), average Sum/h visible_{large group} = 0.39 (SE = ± 0.17); $p = 0.38$, $W = -12.0$, 7 pairs.

P4: We recorded all occurrences of fruit intake rates for focal GLT during March 1998–March 1999. We calculated the average number of seconds that GLT in “large groups” required to consume 1 whole fruit of each of the 8 fruit species. We calculated the same average for GLT in “small groups.” Once again, we omitted 1 fruit species in the comparison because the 3 small groups never fed at the species (*Miconia cinnamomifolia*). We used a Wilcoxon signed-rank test to compare consumption duration/whole fruit for each of the 7 fruit species in “small” vs. “large” groups.

Statistics: Average consumption duration (seconds)/whole fruit for 7 fruit species in small vs. large group: Average consumption duration (seconds)/whole fruit_{small group} = 8.2 (SE = ± 3.3), average consumption duration (seconds)/whole fruit_{large group} = 9.4 (SE = ± 2.9); $p = 0.22$, $W = -16.0$, 7 pairs.

Table II lists energy contents for all plant species (except for 9) on which GLT spent ≥ 1 min feeding. Calorimetry results from duplicate trials within species differed by < 1%. We found a significant positive correlation between the energy content per g of dry fruit matter and

Fig. 3. Average percent time that adult group members and juvenile/subadult group members spent feeding on plant matter, relative to group size ($n = 8$ groups). In the mixed model, the interaction between age and group size significantly influenced time spent eating plant matter, such that juveniles/subadults in larger groups spent more time consuming plant matter than those in smaller groups ($p = 0.01$, $F_{1,219} = 6.36$).

percent time consuming the fruit species (Spearman correlation, $r_s = 0.58$, $p = 0.01$).

Percent Time Spent Consuming Animal Prey

Focal individuals ate prey 1099 times during the study. Of those, 63 were the result of food shares among GLT. Of the time spent consuming identifiable prey, 75% was spent consuming orthopterans, insects commonly eaten by GLT and other callitrichids (Coimbra-Filho, 1981; Dietz *et al.*, 1997; Peres, 1993). GLT also ate walking sticks, cockroaches (Order Blattodea), frogs, lizards, spiders, and caterpillars. We identified the following insects from our collection of 39 samples of wings: Blattodea, Blaberidae, *Epilampra* sp., unknown sp. 1; Orthoptera, Gryllidae, Eneopterinae (?), brown cricket sp. 1; Orthoptera, Tettigoniidae, Phaneropterinae, green katydid sp. 1, 2; Orthoptera, Tettigoniidae, Pseudophyllinae, brown katydid sp. 1, 2, 3, 4 and leaf-mimic katydid sp. 1. Of the 39 samples, 6 were blattodeans (cockroaches), 1 was unidentified and 32 were orthopterans, most commonly 1 species from the Tettigoniidae, Pseudophyllinae (brown katydid species 1).

Table V lists the variables tested in the model to predict monthly percent time eating prey. There was very little variation in percent time eating prey among GLT (adult: $SE = \pm 0.2\%$, juvenile/subadult: $SE = \pm 1.1\%$). The significant variables predicted 8% of the variation in percent time eating prey ($r^2 = 0.08$). The behavioral characteristic, percent time searching for prey, had the greatest influence on percent time consuming prey, explaining 3% of the variation in percent time spent consuming prey. As

Fig. 4. Average percent time spent searching for animal prey and eating animal prey for 26 adults and 8 juveniles/subadults. In the mixed model, time spent searching for prey significantly influenced time spent eating animal prey, such that the greater time GLT spent searching for prey, the greater time they spent consuming prey ($p < 0.005$, $F_{1,171} = 9.00$). There was no significant interaction between age and time spent searching for prey.

predicted, the more time GLT searched for prey, the more time they consumed prey (Fig. 4). In a post hoc test, we added the interaction between age and percent time spent searching for prey into the model predicting percent time spent eating prey. There was no significant effect of the interaction between searching and age, on percent time spent consuming prey. Minor (but statistically significant) influences on percent time eating prey included percent time in social behaviors and the group average monthly percent time spent in encounters. Each variable had an inverse relationship with percent time consuming prey.

Percent Time Spent Searching for Animal Prey

GLT searched for prey primarily in tree bark, bromeliads, and foliage. Table V lists the variables tested in the model to predict monthly percent time searching for prey. The significant variables in the model predicted 25% of the variation in monthly percent time searching for prey ($r^2 = 0.25$). Age (an individual characteristic) and percent time traveling (a behavioral characteristic) accounted for most of the variation (14% each) in percent time searching for prey. As predicted, juveniles/subadults spent a higher percent time searching for prey than adults. Also, as percent time traveling increased, percent time searching for prey increased (Fig. 5). Average monthly day length had a minor (but statistically significant) influence on monthly percent time searching for prey. Contrary to what was predicted, GLT spent a higher percent time searching for prey during months of shorter day lengths.

Fig. 5. Average percent time spent traveling and searching for prey for 26 adults and 8 juveniles/subadults. In the mixed model, time spent traveling significantly influenced time spent searching for prey, such that the greater time GLT spent traveling, the greater time they spent searching for prey ($p < 0.0001$, $F_{1,171} = 16.76$).

We further investigated the relationship between age and time spent searching for prey by examining the foraging success of adults and juveniles/subadults. Foraging success was defined as time spent consuming prey obtained through searches (excluding food shares)/time spent searching for prey. Average foraging success did not differ significantly between adults and juveniles/subadults (Mann-Whitney U test: $U = 87.0$, $n_{\text{(adults)}} = 26$, $n_{\text{(juveniles/subadults)}} = 8$, $p = 0.50$). But, the variance of foraging success for adults was significantly lower than that for juveniles/subadults (F -test, $F_s = 6.0$, $F_{.05(7,25)} = 2.85$, $p < 0.001$).

DISCUSSION

The objectives of the study were to quantify the energy contents of foods consumed by GLT and to identify characteristics that had the strongest influence on feeding in wild GLT. We tested the influence of characteristics of the 1) individual, 2) group, 3) environment, and 4) other behaviors. Table V is a summary of characteristics that affected feeding behaviors.

Percent Time Spent Feeding on Plant Matter

We found that the group characteristic, group size, had the strongest influence on percent time spent feeding on plants. We found no evidence that the greater time spent feeding by individuals in large groups vs. small groups was for the purpose of compensating for the negative effects of food competition, as seen in other primates (Janson, 1988; van Schaik *et al.*, 1983).

In fact, we found no evidence of food competition. Large and small groups did not differ in terms of percent time spent traveling, average DBH of fruit trees fed from, number of fruit trees fed from, and fruit intake rate. In addition, variation in percent time spent feeding by large vs. small groups could not be explained by variation in territory quality. Therefore, why are individuals in large groups spending more time consuming plant matter than individuals in small groups? We offer a possible explanation related to the benefit of food consumption and the influence of predation.

We compared energy intake and energy expenditure for 7 reproductive females in our 8 study groups (Miller, *in press*). Reproductive females in large groups had 4.3 times the average energy intake of reproductive females in small groups, while energy expenditure did not vary among the females in large vs. small groups (Miller, *in press*). Therefore, reproductive females in large groups may have a greater advantage of translating their net energy gain into offspring than reproductive females in small groups. In addition, we qualitatively compared time budgets of large and small groups (Table III). Besides time spent consuming plant matter, the only other substantial difference in activity budgets between large vs. small groups was the percent time spent stationary. A trade-off seems to exist between percent time spent stationary and percent time spent eating plant matter, such that small groups spent more time stationary and less time eating plant matter than large groups did. We suggest that individuals in small groups may have to spend more time stationary per individual (vs. individuals in large groups) for the purpose of engaging in predator vigilance. Taken together, large groups may have a feeding advantage over small groups, and it may in part be influenced by differential time spent stationary and vigilant. Extensive data on time spent vigilant would address our suggestion. Because vigilance behavior is often difficult to quantify, controlled experiments may be designed to test the potential relationship between group size and vigilance behavior. For example, a simulated predator could be presented to groups. Rates at which individuals directed their attention to the location where the predator was previously seen could be compared in small vs. large groups. In addition, as group mass is a more relevant measure of energetic requirements than group size, it would be ideal to collect repeated measures of individual masses each month and include group mass in the feeding models.

Percent Time Spent Searching for Prey and Consuming Prey

Interestingly, there was very little variation among individuals in percent time spent consuming prey, which may indicate a uniform protein requirement among GLT. In addition, there was no significant environmental

influence on percent time spent consuming prey. Adding more specific environmental variables to the model, including seasonal abundance of prey and availability of prey microhabitats, may make the model explaining percent time spent consuming prey more informative.

We found that time the behavioral characteristic, percent searching for prey, most strongly influenced percent time consuming prey. Likewise, we found that individual characteristics (age) and behavior characteristics (time spent traveling) most strongly influenced time searching for prey (Table V). That percent time searching for prey was strongly influenced by individual characteristics (age) is in contrast to percent time eating plant matter, which was most strongly influenced by the group characteristic, group size. These results support our hypothesis that because of the relatively solitary nature of searching for prey, individual characteristics, as opposed to group characteristics, strongly influence percent time spent searching for prey. One GLT typically searches within a microhabitat, e.g., tree bark or a rolled-up palm leaf, for prey, while multiple GLT feed together in fruit trees. Because of the more shared activity of feeding on plant matter, group characteristics most strongly influence percent time spent feeding on plant matter.

Prey are found at relatively low densities within a microhabitat (tree bark or leaf), whereas fruits are found at relatively high densities in fruit trees. Therefore, characteristics of the group may drive feeding at high-density patches, e.g., fruit tree, where many members are allowed to feed (e.g., Isabirye-Basuta, 1988). Conversely, characteristics of an individual, such as foraging ability, may drive feeding at low-density food patches, e.g., prey microhabitat, where exclusion of others occurs. Comparing how individual or group characteristics influence feeding across primate species with different food preferences or as conspecifics seasonally switch food preferences, e.g., fruit vs. prey, would provide additional relevant data for our hypotheses.

Implications of Factors Influencing Feeding

Flexibility in social systems may relate to a dependence on foods with unpredictable availability (Ferrari and Lopes Ferrari, 1989). Intergroup variation in the expression of different social systems has been noted for tamarins and lion tamarins (Dawson 1977, 1979; Dietz and Baker, 1993; Ferrari and Lopes Ferrari, 1989; Terborgh and Goldizen, 1985). Marmosets have more stable social systems and depend on gum, a relatively predictable food source (Ferrari and Lopes Ferrari, 1989). Dawson (1979) found that an upland group of Panamanian tamarins (*Saguinus geoffroyi*) increased their range size during resource shortage in the dry season and had a less stable

group composition, whereas the lowland group did not increase its range size and had a more stable group composition. In our study, we found that more than half of the adult trees did not fruit, which may indicate temporal instability of food sources. The temporal instability in food sources may, in part, explain intergroup variation in tamarin social systems and the large size of GLT territories versus the smaller territories of marmosets (Ferrari and Lopes Ferrari, 1989).

Quantifying proximate pressures acting on primate behaviors allows development of casual models to explain the relationship between ecology and social structure (Janson and van Schaik, 1988). We identified time spent traveling, age, and group size as the factors accounting for the most variation in feeding. We also determined that percent time spent feeding on plant matter was related to the energy content of the foods consumed. Altmann (1998) found a direct link between the diet of yellow baboons (*Papio cynocephalus*) at 30–70 wk of age and their survival and reproductive success. We found that age influenced percent time spent searching for prey and we found a high variation in the foraging success of young GLT. The next step would be to investigate the degree of variation in foraging success among young GLT and whether it affected their survival and reproductive success. In addition, patchy distributions of resources such as prey microhabitats probably influence ranging patterns within primate populations (Dietz *et al.*, 1997; Neyman, 1977). Another influence on ranging and other population dynamics may be low prey density within each microhabitat, resulting in the solitary hunting style observed in many primate species.

The distinction between group vs. individual effects on feeding behavior is critical to understanding primate foraging strategies. We recognize that one trade-off to observing a large number of GLT was the relatively short duration of observation of each GLT per mo. Taken overall, results from our study emphasize the importance of a distinction between feeding in fruit trees, i.e., high-density patches, where many individuals feed together, and feeding in prey microhabitats, i.e., low-density patches, where a single individual feeds. Group characteristics had a greater influence on percent time spent feeding on plants, while individual characteristics had a greater influence on percent time spent searching for prey.

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