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Diet and Feeding Ecology of *Ateles chamek* in a Bolivian Semihumid Forest: The Importance of *Ficus* as a Staple Food Resource

Annika M. Felton · Adam Felton · Jeff T. Wood · David B. Lindenmayer

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Abstract We describe temporal patterns of food consumption by Peruvian spider monkeys (*Ateles chamek*) in a semihumid forest in lowland Bolivia. We assessed dietary composition in relation to temporal variation in abundance, duration, and synchrony of different food items in their home range. We collected data from September 2003 to September 2004, in the forestry concession La Chonta, Department of Santa Cruz. Throughout the period of detailed feeding data collection (February-September 2004), *Ateles chamek* used *Ficus* as a staple food resource. Figs constituted almost 50% of their diet in terms of total time spent feeding, and subjects consumed them to a great extent even during times of high overall food availability. This is contrary to the general expectation that for Neotropical frugivores, *Ficus* is a fallback food in times of fruit scarcity, rather than a staple food resource. Surprisingly, despite being considered ripe fruit specialists, *Ateles chamek* spent 18% of their feeding times eating unripe figs. *Ateles chamek* consumed unripe figs all through the year, including periods when ripe figs and other ripe fruit were abundant. We identify other important fallback foods for *Ateles chamek* in the forest, in particular the ripe fruit of *Myrciaria* sp.

Keywords *Ateles chamek* · diet · *Ficus boliviana* · fig · unripe fruit

Introduction

Over the course of a year the majority of tropical forests experience seasonal variation in rainfall, temperature, and day length (van Schaik *et al.* 1993), resulting

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A. M. Felton · A. Felton · J. T. Wood · D. B. Lindenmayer
Fenner School of Environment and Society, Australian National University, Canberra 0200, Australia

A. M. Felton (✉) · A. Felton
Instituto Boliviano de Investigación Forestal (IBIF), Santa Cruz de la Sierra, Bolivia
e-mail: Annika.Felton@anu.edu.au

in distinct and predictable periods with varying production, duration, and synchrony of food resources that primates can consume (Janson and Chapman 1999; van Schaik *et al*. 1993). During periods of relatively low abundance of their preferred food, primates must be able to alter their dietary composition or activity patterns, or both, if they are to avoid negative impacts on health and reproduction (van Schaik *et al*. 1993).

Spider monkeys (*Ateles* spp., subfamily Atelinae) are canopy-dwelling frugivores in Neotropical forests that in many areas experience marked seasonal differences in rainfall and food availability (Di Fiore *et al*. in press). They are ripe fruit specialists, spending 75–90% of their foraging time consuming predominantly ripe fruit (Cant 1990; Castellanos 1995; Chapman 1987, 1988; Dew 2001; Kinzey 1997; Klein and Klein 1977; Symington 1988; van Roosmalen 1985; Wallace 2005). However, spider monkeys can temporarily switch to alternative diets if conditions require them to do so (Chapman and Chapman 1990). During periods of fruit scarcity, they may rely on flowers and leaves (Chapman 1987; Symington 1988; van Roosmalen 1985), unripe fruit in combination with leaves (Milton 1993; Wallace 2005), or rarely, seeds (Cant 1990).

An important fallback food for Atelinae during times of food scarcity is ripe figs (syconium) of *Ficus* (Terborgh 1983). *Ficus* trees are renowned for the tendency to provide food out of synchrony with the rest of the forest (Janzen 1979). Though primates rarely prefer figs in times of plenty (Milton *et al*. 1982; Shanahan *et al*. 2001), researchers often consider them to be a keystone resource owing to large crop sizes, their accessibility to small and large primates, and their reliability in times of general fruit scarcity (Shanahan *et al*. 2001; Terborgh 1983, 1986).

Descriptions of the diets of frugivorous primates have traditionally contrasted the relative importance of different food items by the time spent feeding on them. Though one can use other methods that assess the nutritional or mineral content of the diet to elucidate the motivations underlying the feeding ecology of a species, time-based assessments are excellent means to compare populations in different forest types and the relative dominance of different food resources in their diet. We describe the diet of a community of Peruvian spider monkeys (*Ateles chamek* Humboldt 1812) in a semideciduous humid forest in lowland Bolivia. We describe seasonal changes in dietary composition in terms of the proportion of time spent feeding and interpret this in relation to the temporal variation in abundance, duration, and synchrony of different food items in their home range. We assess the relative importance of *Ficus* in their diet and how the temporal pattern of its use is related to the abundance of other food resources.

Methods

Study Area and Subjects

Felton conducted the field study in the lowland subtropical semihumid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia (Fig. 1). The study area (S: 15 36 26.3 to 15 37 44.5 and W: 62 46 58.9 to 62 47 55.7) is located in the 100,000-ha forestry concession La Chonta,

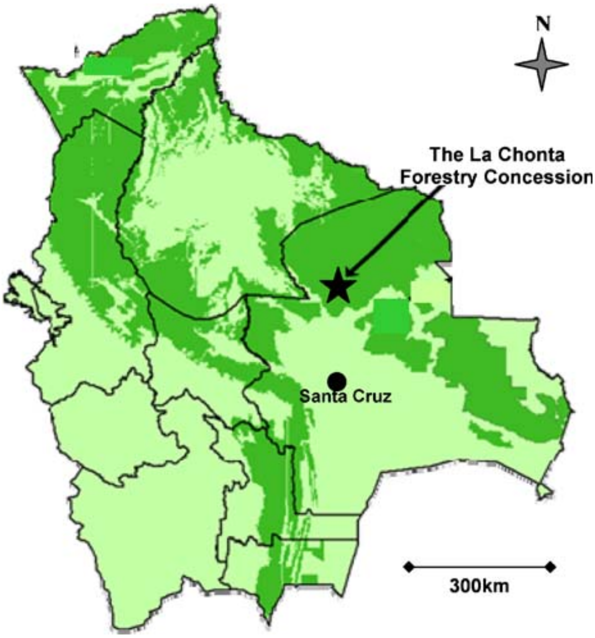


Fig. 1 Map of the La Chonta forestry concession, Bolivia, South America. Dark shading: moist forest; light shading: other vegetation types.

which is owned and managed by Agroindustría Forestal La Chonta Ltda. The forest varies in altitude from 230 m to 390 m with an average elevation of 320 m. The area is a continuation of the Brazilian Shield with low-fertility soils consisting of oxisols, ultisols, and inceptisols (Park *et al.* 2005). Average annual precipitation for La Chonta is 1570 mm and average annual temperature is 25°C. Between November 2003 and October 2004 La Chonta received 1628 mm of rainfall. The seasonal distribution of rainfall during the study was representative of the average monthly rainfall for the forest, with the possible exception of the end of the dry season when rainfall was below average (Fig. 2). The study area is *ca.* 5 km from the northern edge of the concession and ≥2 km from recent logging disturbance (harvesting

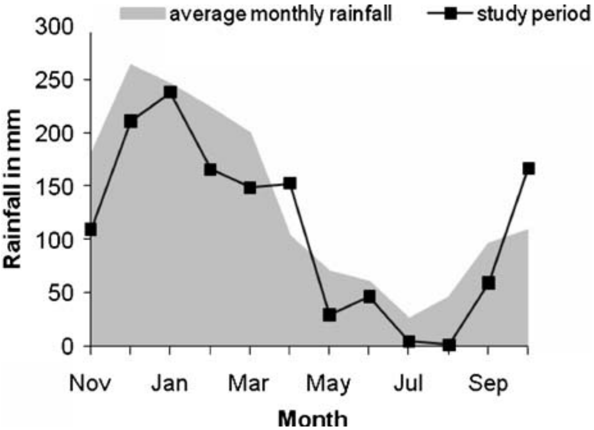


Fig. 2 Average monthly rainfall for the La Chonta forestry concession, and specific rainfall data for study period from Agroindustría Forestal La Chonta Ltda.

2001–2002). The closest active timber harvesting was ≥8 km to the west of the study area and was not audible to the researchers.

Ateles chamek is the most abundant primate species in this section of the Guarayos Forest Reserve (Wallace *et al*. 2000). Four other primate species occur in La Chonta: *Alouatta* cf. *seniculus, Aotus azarae, Callithrix melanura,* and *Cebus apella. Ateles* spp. live in fission-fusion societies in which individuals from a large community associate on a daily basis in small subgroups that change size and membership frequently (Di Fiore and Campbell 2007). The La Chonta community comprised 55 individuals at the end of the study period.

Study Design and Vegetation Survey

During habituation of the community (duration 5 mo) we established a network of trails (40 km in total) in the study community's home range, which covered an area of *ca*. 360 ha. We used the network for daily follows, monthly phenology surveys, and a one-off vegetation survey. We collected phenology data ≤5 m of each side of the trails and additional trails immediately abutting the home range (total length 56 km). To describe the vegetation in the home range and to obtain basal area information of monitored food species, at the end of the study period we established 71 vegetation plots (100 m long, 10 m wide). We distributed plots within the trail network in relative proportion to the different vegetation types that we had visually categorized during the course of the year. In the plots we identified all trees ≥10 cm diameter-at-breast height (DBH) and measured their diameters.

Phenology Survey

In the survey population we included plants belonging to plant genera known or presumed to be eaten by *Ateles*. When possible we included ≥30 individuals of each species in the survey, selected randomly along survey trails. We initially tagged trees of ≥10 cm DBH, mature palms and lianas, and then monitored them approximately once a month to coincide with the completion of focal individual follows. We collected phenology data from November 2003 to October 2004. Due to severe storms we did not collect data in January. During each survey we noted the presence of ripe fruit, immature fruit, and flowers. We used differences in fruit size, color, and consistency to differentiate between immature and ripe fruits. Unripe fruit includes items ranging from emerging fruit (very small and green) to fruit of mature size but lacking ripe coloration or texture.

Because the contribution of different species in the phenology survey did not represent their actual densities in the forest, we calibrated monthly food availability estimates (Chapman *et al*. 1994). Because the basal area of a tree is an easy and reasonably accurate index of its fruit crop sizes (Leighton and Leighton 1982; McDiarmid *et al*. 1977; Peters *et al*. 1988), we used basal area information to calculate a monthly index of general food availability. We calculated species-specific basal area values as a mean for the entire home range, averaging across the 3 vegetation types according to their relative contribution. For dioecious tree species, such as *Pseudolmedia laevis* and 25 other species in the study area (Bawa and Krugman 1991; Bawa *et al*. 1985; Justiniano *et al*. 2003; Kubitzki and Kurz 1984;

Mostacedo *et al.* 2003; Ressell *et al.* 2004), we assumed that half of the trees were female and produced fruit, per Fredericksen *et al.* (1999). For trees, we calculated a monthly index T:

$$\text{Index } T = \sum\nolimits_i (p_i \times BA_i) * 100$$

wherein p_i is the proportion of surveyed individuals of species i that carry an edible phenophase at a given time, and BA_i is basal area/ha of species i. We also broke down index T into different categories: ripe fruit, unripe fruit, ripe figs, unripe figs, and flowers. Owing to the relatively long interval between surveys (*ca.* 30 d), we did not observe the fate of some documented unripe fig crops as they had ripened and been eaten before the subsequent survey. Therefore, we have estimated the date when the ripe crops would have been available by arbitrarily choosing the midpoint between consecutive surveys. We present the data points as projected data. We did this only for species of *Ficus* because we treated the genus separately. In the general tree fruit index, we include many species, and the effect of unripe crops with undocumented fate will be smaller.

Because the trunks of arboreal palm trees generally do not grow incrementally (Schatz *et al.* 1985), we did not measure their diameter and therefore could not include them in index T. Instead we calculated a separate index P of palm food availability based on their densities:

$$\text{Index } P = \sum\nolimits_i (p_i \times d_i) * 100$$

wherein d_i is density of species i (individuals/ha). We included a tree or palm species in index T or P if 1) we recorded it as a food source for *Ateles chamek*, 2) it was included in the phenology trail, and 3) it was present in the vegetation survey plots to supply basal area or density information. We did not include lianas in the vegetation survey, so no abundance data are available. For liana species recorded as food sources for *Ateles chamek*, we therefore calculated a simple monthly index of percentage of surveyed lianas bearing ripe fruit (index L).

Feeding Observations

We identified and measured (DBH) all feeding trees of *Ateles chamek* between September 2003 and September 2004. After habituation, we systematically collected detailed feeding data from February 2004 to September 2004. Because our unit of interest was the food intake per individual per day, we conducted continuous observations of the same focal individual from dawn (0545–0615 h) to dusk (1745–1830 h). We established a list of 18 readily identified focal individuals. We identified them by facial and bodily markings. Eight of them were adult males and 10 were adult females that were lactating or pregnant, and/or caring for a dependent juvenile. When possible, we followed 10–15 individuals for 1 whole day each month, over 20 d, and alternated between male and female focal individuals on a daily basis. We refer to days when we successfully followed the focal individual for >10 h as full. We refer to days when we followed the focal individual <10 h the day (minimum of 5 h) as partial.

We collected data continuously on the focal individual's activities, including even short feeding events. We noted the exact start and end time of each feeding session (event). We recorded the plant parts eaten: ripe fruit/fig, unripe fruit/fig (separated into emerging, young, and mature fruit), flower, young leaf, mature leaf, or other. Near-ripe fruit and figs are included in the ripe category. We identified and tagged all plants from which either the focal individual or other members of the subgroup were eating.

Data Analysis

We calculated proportions of dietary items and plant species based on the total amount of time spent feeding by focal individuals. We excluded partial follow days with <60 min of feeding observations from the percentages (daily feeding time of full days averaged 155 min, range 52–303 min).

We calculated an electivity index (E_i) to determine food species preference in the diet of *Ateles chamek*. The index is calculated as follows (Krebs 1989):

$$E_i = (r_i - n_i)/(r_i + n_i)$$

wherein r_i is the percentage of species i in the diet (based on time spent feeding), and n_i is the relative abundance of species i in the spider monkey home range (based on basal area/ha). We adjusted basal area values for dioecious species. Index values range from −1 (avoided) to + 1 (highly selected).

We tested whether there is a statistical difference between months in time the focal individual spent feeding during full days via linear regression analysis, including sex of the focal individual as a predictor. To assess whether different aspects of food availability were driving daily time the focal individual spent feeding during full days, we ran regression models using the following candidate variables: availability of ripe figs, unripe figs, ripe non-fig fruit, unripe non-fig fruit, flowers, and the sex of the focal individual. We matched daily data on time spent feeding with the food availability indices produced from phenology surveys conducted on dates (≤2 wk) closest to the follow days. We selected regression models by considering all possible subsets of predictors and then choosing the model with the smallest value for the Akaike Information Criteria (Akaike 1974). We ran 2 similar regression analyses with time spent feeding on figs in total and time spent feeding on ripe figs as response variables, with the same candidate variables as listed above. We checked for departures from our assumptions by inspecting QQ plots of residuals, and plots of residuals against fitted values. We treated all full follow days as independent data points because the estimated correlation between follow days for the same individual was negative and negligible.

Results

Vegetation Structure in Home Range

The study community's home range was primarily tall forest (*ca.* 60% of study area), with smaller areas of low vine forest (35%) and chaparral (<5%) and swamp (<1%). The tall forest is characterized by greater tree density, basal area, and mean height of trees than the low forest and the chaparral (Table 1). Further, the 3 vegetation types contain different dominant tree species (Table 1).

Table 1 Vegetation structure of the 3 main forest types in the home range of the study community of *Ateles chamek* at La Chonta

Mean of plots	Tall forest (60%)	Low forest (35%)	Chaparral (5%)
No. of plots surveyed	39	22	2
Tree density (no. of trees/ha)	491±15	394±23	385±5
Basal area (m^2/ha)	29.8±2	20.3±1.9	20±3.1
Height (m)	12.4±0.3	10.5±0.3	10.1±0.2
Liana infestation index (0–3)	1.4±0.1	1.8±0.4	1.7±0.6
Species diversity	20.4±0.8	19.8±0.8	20.5±2.5
Dominant species (density)	*Pseudolmedia laevis* (Moraceae)	*Ampelocera ruizii* (Ulmaceae)	*Cariniana ianeirensis* (Lecythidaceae)
	Ocotea sp (laurel, Lauraceae)	*Gallesia integrifolia* (Phytolaccaceae)	*Schizolobium parahyba* (Ceasalpiniaceae)
	Socratea exorrhiza (Arecaceae)	*Terminalia oblonga* (Combretaceae)	*Ceiba pentandra* (Bombaceae)
Dominant species (basal area)	*Pseudolmedia laevis* (Moraceae)	*Pseudolmedia laevis* (Moraceae)	*Urera baccifera* (Urticaceae)
	Hura crepitans (Euphorbiaceae)	*Urera baccifera* (Urticaceae)	*Pseudolmedia laevis* (Moraceae)
	Ficus trigona (Moraceae)	*Pouteria macrophylla* (Sapotaceae)	*Ocotea* sp. (negrillo, Lauraceae)

Results are plot means ± 1 SE. Numbers in parentheses indicate approximate contribution of each forest type within the home range. Eight plots that contained a mixture of different forest types are not included.

Phenology

We initially included 2105 individual plants in the monthly phenology surveys. During the year we excluded 103 plants because they died or we could not properly observe their canopies from the ground. Seventy-two species of trees and 20 species of lianas are represented. Of the 92 species, we observed that *Ateles chamek* used 44 during the year: 34 species of trees and 10 species of lianas. They also fed from 11 additional plant species that we did not include in the surveys: 1 major food source (*Heliocarpus americanus* L., Tiliaceae) and 10 minor food species. The fruiting periods of the species included in surveys are in Appendix.

The seasonal changes in food availability from November 2003 to October 2004 are in Fig. 3. When phenology surveys began in the wet season, ripe fruit were abundant. In early February we detected a paucity in fruit abundance (Fig. 3). During the period of detailed feeding data collection (February–September), there are 3 distinct phenological periods (Table 2). A period of relatively high ripe fruit abundance occurred during the late wet season, which was followed by 10–14 wk of tree fruit scarcity during the early-to-mid dry season. The second half of the period was particularly poor in ripe fruit when neither trees nor lianas provided many ripe crops in the home range. During this time, *Myrciaria* sp. (local name, *sahuinto*) was the primary source of ripe fruit in the home range. The species also fruited during the short period of general fruit scarcity in early February. After the long period of fruit scarcity, ripe fruit was abundant again during the late dry-to-early wet season.

Lianas had 1 period of ripe fruit production that occurred with a month's time lag to that of trees (Fig. 4). Palms provided ripe fruit at an almost continuous level

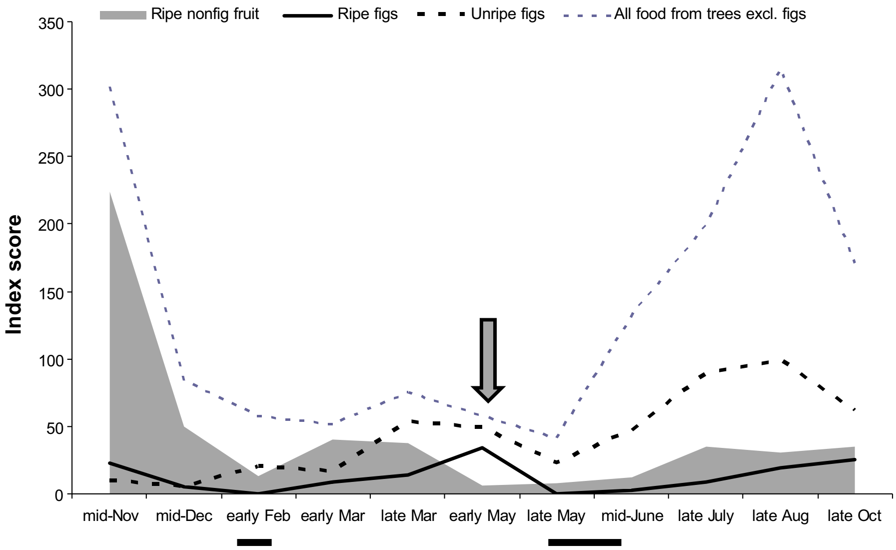


Fig. 3 Availability of spider monkey food items from tree species in La Chonta, November 2003–October 2004 (31 tree species included; see Methods for index score explanation). All food from trees, excluding figs, includes edible flowers and ripe and unripe fruit. The gray arrow indicates period of asynchronicity in availability of ripe figs versus ripe nonfig fruit. Lines under graph indicate periods of ripe nonfig fruit scarcity when ripe figs were also scarce.

Table 2 Three phenological periods during the duration of detailed data collection of feeding behavior of *Ateles chamek* in La Chonta, February-September 2004

	Late wet	Early-mid dry	Late dry-early wet
Months	February to mid-April	Mid-April to early July	Early July to mid-September
No. of surveys conducted	3	3	2
Mean phenology score of all ripe tree fruit[a]	38 (50)[b]	22	48
Range of scores between surveys	14–52	10–41	43–53
Major sources of ripe fruit available[c]	*Spondias mombin* *Pouteria nemorosa* (i) *Jacaratia spinosa* *Ficus boliviana* (ii) *Inga edulis* *Alibertia verrucosa* *Myrciaria* sp. *Ampelocera ruizii* *Sapium glandulosum*	*Myrciaria* sp. *Ficus trigona* (iii) *Ficus boliviana* (iii)	*Dendropanax arboreus* *Ficus trigona* *Guazuma ulmifolia* *Myrciaria* sp. *Ficus boliviana* *Didymopanax morototoni* *Pouteria macrophylla*

[a] Phenology index T (see Methods for explanation of score calculation).

[b] Values in parentheses: mean score when the low value of February is excluded.

[c] Species listed in order of abundance: i) end of February only; ii) large peak at the end of period; iii) at the beginning of period only.

throughout the study period, with peaks overlapping with periods of high tree fruit abundance (Fig. 4). Unripe figs (Fig. 3) and edible unripe non-fig fruit were also available continuously throughout the year.

Of the 4 species of *Ficus* in the phenological survey, *Ficus boliviana* and *F. trigona* represented 91% of available crops. Species of *Ficus* periodically provided ripe fruit when other trees did not (Fig. 3). However, during the 2 dips in general tree fruit availability, ripe fig availability also declined (Fig. 3). When ripe fig crops are projected from observed unripe crops with unknown ripening date, only 2–6

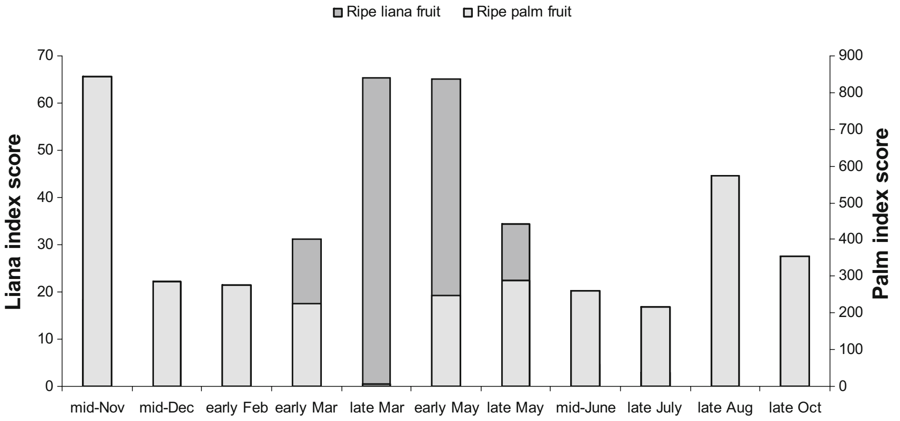


Fig. 4 Availability of ripe liana fruit (10 species) and ripe palm fruit (4 species) at La Chonta, November 2003–October 2004 (see Methods for index score explanation).

additional trees presented ripe crops during the long period of fruit scarcity. In comparison, 10–13 additional ripe fig crops occurred during the late dry-to-early wet season (August–September). During the fruit-poor months of late May and June, the scarcity of ripe figs corresponded with a similar lack of ripe figs in the diet of *Ateles chamek*, which suggests that the sample of fig trees in our survey was representative for the community's home range in general.

During the months of data collection on feeding, the 2 dominant species of *Ficus* (*F. trigona* and *F. boliviana*) showed a bimodal fruiting pattern that overlapped in time with each other. Both species peaked in fruit production in early May and late August to October.

Feeding Observations on *Ateles chamek*

From February to September, we conducted 863 h of focal subject observations. We recorded 904 different feeding events for focal individuals, ranging in duration from 0.2 min to 204 min, and amounting to 175 h of feeding observation (collected during 32 full and 11 partial follow days for females; 19 full and 8 partial follow days for males). Time the focal individual spent feeding during full follow days differs significantly between months and sexes (combined model: adjusted $R^2=46.4$, mo $p<0.001$, sex $p<0.001$). July and August had the highest recorded daily feeding time (mean 180 min/d±11 min), while late May and June had the lowest (mean 100 min/d±14 min). Females spent more time feeding than males did (females: mean 169 min/d±10 min; males: mean 132 min/d±12 min).

Overall Diet

Feeding data of *Ateles chamek* reveal that fruits constituted 82% of the total diet in terms of time spent feeding (Appendix). Focal individuals spent 32.3% of the total feeding time on ripe non-fig fruit, 26.8% on ripe figs, 5.1% on unripe non-fig fruits, and 17.8% on unripe figs.

For focal individuals, leaf material constituted 13% of the total feeding time, most of which was leaf buds (52% of leaf consumption time) and young leaves (26%). Flowers were a seasonal food for *Ateles chamek* and amounted to 4.7% of total feeding time. They also consumed other vegetative material such as palm heart, dead wood, aerial roots, stalks, and bark. These items made up only 0.2% of all feeding time (Appendix). We also observed invertebrates being consumed on 8 occasions (<1% of feeding events). Five of the events occurred during habituation when *Ateles chamek* fed for long periods of time on caterpillars among the leaves of *Terminalia oblonga*.

Dietary Diversity and Prominent Plant Species in the Feeding Time Budget

During the 12 mo of data collection on food sources, we observed *Ateles chamek* to eat 105 different types of plant items, belonging to 63 species, representing 37 families (Appendix). In the diet of focal individuals, Moraceae was the family represented with most species. In terms of time spent feeding, Moraceae also topped the list (61.2% of total feeding time).

The fruits of just 2 tree species comprised almost 50% of their total time spent feeding. The tree species upon whose fruits they spent the most time feeding were *Ficus boliviana* (28.6% of time), *F. trigona* (20.3%), *Myrciaria* sp. (10.3%), and *Pseudolmedia laevis* (9.4%; Appendix). *Ficus* was absent from the diet in only 8 of the 51 full follow days, 7 of which occurred during the period of fruit scarcity in June.

In terms of time spent feeding on ripe fruit, the primary source was *Ficus trigona* (30.2% of time spent eating ripe fruit) followed by *Myrciaria* sp. (17.4%) and *F. boliviana* (14.5%; Appendix). Palm fruit constituted only 2% of time eating ripe fruit. The equivalent value for liana fruit was 7.6%. Of the time spent feeding on unripe fruit, 68.1% was spent in *Ficus boliviana*. Besides *Ficus boliviana*, focal individuals ate unripe fruit mainly from *Pouteria nemorosa* (11.9%: medium-ripe fruit), *Pseudolmedia laevis* (9.7%: emerging and young fruit), and *F. trigona* (8.7%: small immature figs; Appendix). The medium-ripe fruit focal individuals harvested from *Pouteria nemorosa* were from trees that appeared to have a damaged crop of fruit the year of sampling: fruits were water laden and rotting on the branch, did not fully ripen and subjects often rejected them.

The time focal individuals spent eating figs was almost equally divided between the 2 most common species of *Ficus* in the forest: 48.2% for *F. boliviana*, and 50.1% for *F. trigona*. The remaining portion of total fig eating time focal individuals spent in 3 rare species of *Ficus* (*F. eximia, F. pertusa,* and *F. gomelleira*). Notably, 65% of time they spent eating in *Ficus boliviana* was on unripe figs, while the equivalent value for *F. trigona* was 10%. *Ficus boliviana* was the source of 87.8% of time spent feeding on unripe figs in general.

The majority of the time focal individuals spent eating young leaves were in *Ficus* (*F. boliviana* 43.4%, *F. trigona* 4.7%). *Pseudolmedia laevis* provided the most flowers and flower buds (84.7% of flower feeding time; Appendix).

We may have underestimated the relative importance of 11 other species, which are known or presumed food sources for *Ateles* (*Alibertia verrucosa, Ampelocera ruizii, Attalea phalerata, Brosimium guadichaudii, Cordia alliodora, Dendropanax arboreus, Didymopanax morototoni, Guarea guidonia, Inga edulis, Syagrus sancona,* and *Talisia esculenta;* Wallace 1998, *pers. obs.*), because their fruiting periods overlapped only partially or not at all with behavioral data collection. Owing to the damaged crop of *Pouteria nemorosa*, it is also potentially underestimated.

Feeding Preferences

For comparison with other studies, we present preference results at the generic level (Table 3). However, because most genera are represented by only 1 species we interpret results at the specific level. The locally rare *Virola sebifera* has the highest electivity index (EI), followed by *Myrciaria* sp. and *Batocarpus amazonicus* (Table 3). *Ficus boliviana* also has a high EI and ranked as 7 among the 29 genera. Subjects used *Jacaratia spinosa* and *Didymopanax morototoni* in accordance with their abundance in the forest (EI close to 0) and fed on several species that were sources of leaves less often than expected relative to their abundance (Table 3). Only 1 palm species (*Syagrus sancona*) had a positive EI even though focal individuals ate only its flowers. Fruit-providing palms had EIs close to 0 (Table 3).

Table 3 Electivity indices for genera included in the diet of *Ateles chamek* in La Chonta

Family	Genus	Cat.[a]	No. of spp.[b]	BA/ha[c]	%BA/ha[d]	EI[e]	EI rank	*T* Rank[f]
Myristicaceae	*Virola*	T	1	<0.01	0.02	0.91	1	22
Myrtaeae	*Myrciaria*	T	1	0.17	0.63	0.88	2	3
Moraceae	*Batocarpus*	T	1	0.07	0.26	0.78	3	9
Tiliaceae	*Heliocarpus*	T	1	0.07	0.26	0.81	4	10
Sterculiaceae	*Guazuma*	T	1	0.13	0.48	0.76	5	7
Arecaceae	*Syagrus*	P	1	3.54	0.78	0.61	6	30–33
Moraceae	*Ficus*[g]	T	3	3.33	12.70	0.59	7	1, 2, 27
Mimosaeae	*Inga*	T	1	0.10	0.37	0.57	8	13
Euphorbiaeae	*Sapium*	T	1	0.18	0.69	0.36	9	12
Araliaceae	*Dendropanax*	T	1	0.32	1.22	0.31	10	8
Sapotaceae	*Pouteria*	T	1	0.59	2.26	0.29	11	5
Anacardiaceae	*Spondias*	T	1	0.35	1.32	0.19	12	11
Caricaceae	*Jacaratia*	T	1	0.35	1.34	−0.03	13	14
Araliaceae	*Didymopanax*	T	1	0.04	0.14	−0.05	14	27–29
Arecaceae	*Attalea*	P	1	1.13	0.25	−0.08	15	24
Arecaceae	*Astrocaryum*	P	1	2.33	0.52	−0.14	16	20
Moraceae	*Pseudolmedia*	T	1	4.42	16.85	−0.29	17	4
Sapindaceae	*Talisia*	T	1	0.03	0.10	−0.46	18	38–40
Cecropiaceae	*Cecropia*	T	1	0.02	0.06	−0.50	19	43–44
Chrysobalanaceae	*Hirtella*	T	1	0.07	0.28	−0.53	20	30–33
Malvaceae	*Ceiba*	T	2	0.32	1.23	−0.70	21	25, 50
Rubiaceae	*Alibertia*	T	1	0.08	0.30	−0.82	22	41–42
Moraceae	*Brosimum*	T	1	0.11	0.40	−0.83	23	38–40
Arecaceae	*Socratea*	P	1	25.29	5.60	−0.85	24	19
Urticaceae	*Urera*	T	1	0.49	1.85	−0.87	25	27–29
Ulmaceae	*Ampelocera*	T	1	1.58	6.04	−0.91	26	23
Rutaceae	*Zanthoxylon*	T	1	0.08	0.30	−0.92	27	45–49
Combretaceae	*Terminalia*	T	1	1.67	6.35	−0.97	28	30–33
Caesalpiniaceae	*Caesalpinia*	T	1	0.31	1.20	−0.98	29	45–49

[a] Category of food source: T = tree; P = palm.

[b] Number of species included.

[c] Basal area m^2 /ha.

[d] Percentage of the total basal area recorded in vegetation survey. For palms, density and %density are shown and used instead of basal area.

[e] Electivity Index (see Methods for explanation).

[f] Rank according to % of total time spent feeding, listed in Appendix.

[g] On a species basis, *Ficus boliviana* ranks 6; *F. trigona,* 9; and *F. pertusa,* 23. No basal area information was available for other rare species of *Ficus*.

Seed Handling

Focal individuals ingested whole seeds and defecated them intact in 98% of feeding events. The exceptions were 3 large-seeded palms (*Socratea exorrhiza, Astrocaryum murumuru,* and *Attalea phalerata*). *Ateles chamek* systematically spat out palm seeds when feeding on the ripe pulp. In no instance did we observe mastication of seeds. In some cases *Ateles chamek* ingested small emerging fruit whose seeds may have been vulnerable to digestion owing to their immaturity (*Ficus boliviana* 3.8% of fruit/fig feeding time; *F. trigona* 0.5%; and *Pseudolmedia laevis* <0.1%).

Monthly Changes in Dietary Composition

The relative proportions of dietary items varied among months (Fig. 5). Fruit and figs contributed >70% of the diet in all months except June (53%), when *Ateles chamek* fed more on leaves and flowers than in other months. The proportion of figs in their diet varied from 2% to 73% (Fig. 5). Unripe fruit/figs constituted >10% of the feeding time in 5 of the 8 mo of detailed data collection, and was >40% of it in 2 mo (March 43%, May 45%). The proportion of leaf material in their diet varied from 0 to 32% (Fig. 5). Flower consumption varied from 0–14% of monthly feeding time, with the peak overlapping with that of leaf consumption (June).

The food sources that contributed to ≥5% of the monthly diet in terms of time spent feeding are in Table 4. Two to 6 species each mo qualified to be included, and the time spent feeding on them amounted to 82–96% of the monthly diets. *Ficus boliviana* tops the list, being prominent in 6 of the 8 mo of detailed data collection (Table 4).

Feeding in Relation to Availability

Daily time spent feeding by focal individuals is best explained in terms of 3 significant variables (best regression model included 3 terms): availability of ripe figs, unripe figs, and the sex of the focal individual (combined model: adjusted R^2= 34.6, ripe figs p=0.005, unripe figs p=0.009, sex p=0.002). Hence, the availability of mainly 2 species of *Ficus* influenced the daily feeding time more strongly than the availability of 25 other fruiting species.

Daily time spent feeding on figs in total (ripe and unripe) is best explained in terms of the availability of ripe figs (best regression model included 1 term: adjusted R^2=50.7, ripe figs p<0.001). The same model revealed that there is no significant difference between sexes in time spent feeding on figs in total (p=0.208). One can instead explain the difference between sexes in overall feeding time by females spending significantly more time than males did feeding on ripe figs (best regression

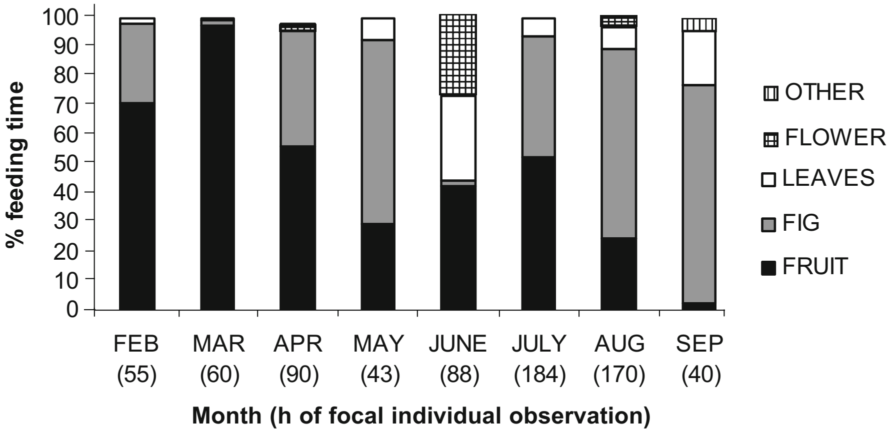


Fig. 5 Monthly proportions of dietary items in feeding time budgets of focal individual *Ateles chamek* in La Chonta.

Table 4 Plant species that contributed to ≥5% of monthly diets in terms of time spent feeding

Family	Scientific name	Percentage of monthly diet								
		Feb	Mar	Apr	May	June	July	Aug	Sept	No. of months[a]
		Late wet season			Early-mid dry season		Late dry- early wet season			
Moraceae	*Ficus boliviana*	20	-	7	40	-	41	18	74	6
Moraceae	*Ficus trigona*	-	-	32	22	-	5	46	-	4
Moraceae	*Pseudolmedia laevis*	-	-	-	-	26	10	18	-	3
Myrtaceae	*Myrciaria* sp.	-	-	-	13	42	13	-	-	3
Anacardiaceae	*Spondias mombin*	-	6	27	-	-	-	-	-	2
Sapotaceae	*Pouteria nemorosa*	16	64	-	-	-	-	-	-	2
Tiliaceae	*Heliocarpus americanus*	-	-	-	5	8	-	-	-	2
Araliaceae	*Dendropanax arboreus*	-	-	-	-	-	8	-	-	1
Arecaceae	*Astrocaryum murumuru*	-	-	6	-	-	-	-	-	1
Bignoniaceae	*Melloa quadrivalvis*	-	-	-	-	-	-	-	12	1
Caricaceae	*Jacaratia spinosa*	-	-	10	-	-	-	-	-	1
Euphorbiaceae	*Sapium glandulosum*	53	-	-	-	-	-	-	-	1
Mimosaceae	*Inga edulis*	-	24	-	-	-	-	-	-	1
Moraceae	*Ficus eximia*	7	-	-	-	-	-	-	-	1
Moraceae	*Batocarpus amazonicus*	-	-	-	-	16	-	-	-	1
Sapindaceae	*Paullinia elegans*	-	-	10	-	-	-	-	-	1
Sterculiaceae	*Guazuma ulmifolia*	-	-	-	-	-	14	-	-	1
Ulmaceae	*Celtis iguanea*	-	-	-	15	-	-	-	-	1
	% of monthly diet[b]	96	94	93	96	93	92	82	86	

[a] Number of months when the species contributed to ≥5% of the total time spent feeding.

[b] Percentage of monthly diet made up of the above listed species.

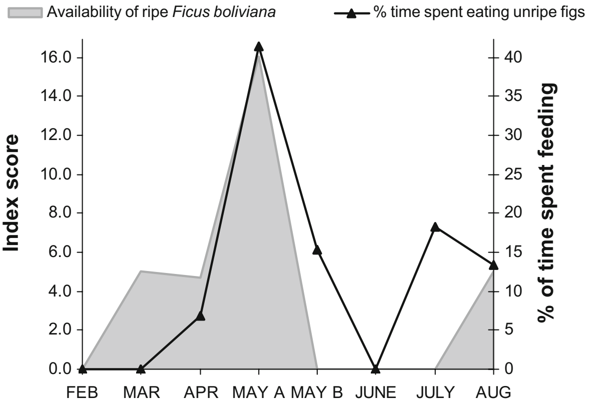
model included 3 terms, adjusted $R^2=26.6$, ripe figs $p=0.009$, unripe fruit $p=0.026$, sex $p=0.038$).

There is no inverse relationship between fig consumption and general ripe fruit availability, as may be expected if figs were merely a fallback food consumed in times of general fruit scarcity. Instead, the second of the 2 peaks in fig consumption overlapped with the peak in ripe nonfig fruit availability in the late dry-early wet season. Contrary to expectations, subjects consumed unripe figs (out of which the majority was *Ficus boliviana*) during times of both abundance and scarcity of ripe *F. boliviana* (Fig. 6). The second peak in consumption of unripe figs occurred when ripe nonfig fruits were abundant (July–August). Similarly, the consumption of young leaves was high during the rich period, when subjects harvested young leaves mainly from fig trees and lianas. Conversely, they ate primarily mature leaves during the fruit-scarce period.

Fallback Foods during Period of Fruit Scarcity

During the long period of general fruit scarcity (early-to-mid dry season), *Ateles chamek* consumed ripe fruit of *Myrciaria* sp. (Table 4). *Ateles chamek* fed on items of *Ficus* only in the beginning of this period (ripe figs of *F. trigona* and unripe figs and leaf buds of *F. boliviana*), when they also consumed ripe fruit from the liana *Celtis iguanea*. To supplement the *Myrciaria* diet during the rest of the period, *Ateles*

Fig. 6 Percentage of time spent feeding on unripe figs (88% of which was *Ficus boliviana*) and the availability of ripe *F. boliviana* in home range. We conducted 2 phenology surveys in May (*A*: early May; *B*: mid-late May). Index score = % surveyed trees with ripe crops × basal area.



chamek consumed young leaves and leaf buds of *Batocarpus amazonicus*, mature leaves of *Heliocarpus americanus*, and flower buds of *Pseudolmedia laevis*.

Discussion

By studying *Ateles chamek* in the forest of La Chonta we have discovered some new aspects of ateline biology. First, *Ficus* appears to be a staple, not a fallback food, for *Ateles chamek* in this forest. Second, *Ateles chamek* spend more time feeding on unripe fruit pulp than previously observed (Di Fiore *et al.* in press). Surprisingly, *Ficus* was the predominant source of unripe fruit, which subjects harvested despite the fact that ripe figs and other ripe fruits were available at the time. We compare our results with those obtained from studies of other members of *Ateles*. This approach is justified by previous research that demonstrated that both intra- and interspecific distinctions in ateline feeding ecology are best explained by differences in the local food resources, rather than taxonomic distinctions of the *Ateles* species being considered (Russo *et al.* 2005).

The dietary composition of *Ateles chamek* at La Chonta generally concurs with previous findings on *Ateles* spp. (Table 5). The proportion of fruit in their overall diet falls within the upper range of previous findings, as does the percentage of leaves. During the period of fruit scarcity, *Ateles chamek* consumed fruit from a small number of plant species, supplemented by young and mature leaves and flowers. This observation also corresponds with several other studies (Table 5). *Myrciaria* sp. was a critical source of ripe fruit for *Ateles chamek* during periods of fruit scarcity because the species provided crops when little else was available.

As reported for other Atelinae (Cant 1990; Russo *et al.* 2005; Serio-Silva *et al.* 2002; Terborgh 1983; Wallace 1998), Moraceae was the most important plant family in the diet of *Ateles chamek* in La Chonta, both in terms of number of species and time spent feeding. Three of the top 5 species in their diet belong to the family (*Ficus boliviana, F. trigona* and *Pseudolmedia laevis*). Besides Moraceae, 36 other plant families and 63 different species featured in their diet. Despite the

Table 5 Dietary composition data from 13 studies on *Ateles* spp

No.	Species	% Fr	Monthly range	% R	%U	%S	%L	%F	%O	%Fi	%Ufig	No. of Fi spp.	No. M>5%U	Major lean season resources
1	*A. geoffroyi*	78	14–100	78	-	[e]	11.1	9.8	1.3	29	-	1	0	Flowers and leaves
2	*A. geoffroyi*	57	31–84	57	10[d]	19.5	14.1	1.5	-	7.8[f]	0	3	-	Seeds and ripe figs
3	*A. geoffroyi*	82	69–91	82	-	1[a]	17.2	1	0.6	6.1[h]	-	8	-	-
4	*A. paniscus*	83	54–92	80	3.3	3.1	7.9	6.4	2.7	0.95	-	10	0	Flowers and young leaves
5	*A. belzebuth*	84	78–100	83	0.8[b]	0	7	<0.1	10	3.4	-	-	0	Palm fruit
6	*A. belzebuth*	-	74–100	89	3.2[c]	-	8.3	0	3.2	9.2	-	8	0	Leaves
7	*A. belzebuth*	87	64–100	87	[g]	1.1	9	1	0.7	0.9	0	5	0	No pronounced lean season
8	*A. belzebuth*	79	52–92	-	[i]	0.8[a]	7.7	3.2	10.3	<1[h]	0	5	0	No pronounced lean season
9	*A. belzebuth*	74	55–80	72	-	2[a]	12	5	9	16.5[h]	-	8	0	Young leaves
10	*A. belzebuth*	73	41–96	-	-	-	13	12	1.2	8.1[h]	-	9	-	-
11	*A. chamek*	86	63–98	81	2.7	2	10.7	2.9	0.6	10.7	0.1	6	2	Seed and leaves
12	*A. chamek*	75	54–99	75	-	-	-	-	-	-	-	-	-	Leaf flush, flowers, figs and seeds
	AVERAGE:	78		78	4.0	3.7	10.7	3.9	4.0	8.5	0.0	6		
13	*A. chamek*	83	53–100	59	23	0	13	4.7	0.3	49.5	18	6	7	Leaves, flowers and unripe fruit/figs

All percentages are of total time spent feeding.

Fr = Fruit total; R = ripe fruit; U = unripe fruit pulp; S = seed; L = leaves; F = flowers; O = other; Fi = *Ficus* total; Ufig = unripe figs; No. of Fi spp = number of *Ficus* species in diet; No. M>5%U = number of months with >5% of feeding time represented by unripe fruit in general; - = no information available.

[a] % of plant species.

[b] 1/100th of ripe fruit consumption.

[c] Unripe fruit included in Other but cannot be separated.

[d] Approximate, calculated from data in original paper.

[e] Some seed included in fruit fraction but cannot be separated.

[f] Average for the main study period. Periodical means particularly for dry season diets range 14–45%.

[g] Not quantified rare events involving Aracaeae (1 sp.) and Sapotaceae (1 sp.).

[h] Data from Di Fiore, *et al.* (in press).

[i] Not quantified event involving Aracaeae (1 sp).

Source, study location, and duration: 1) Santa Rosa N. P., Costa Rica, 24 mo (Chapman 1987, 1988); 2) Tikal N. P., Guatemala, 9 mo (Cant 1990); 3) Barro Colorado Island, Panama, 14 mo (Di Fiore *et al.* in press); 4) Voltzberg Nature Reserve, Surinam, 26 mo (van Roosmalen 1985); 5) La Macarena N.P, Colombia, 11 mo (Klein and Klein 1977);6) Ilha de Maraca, Brazil, 22 mo (Nunes 1998); 7) Yasuni N.P, Ecuador, 12 mo (Dew 2001, 2005); 8) Yasuni N.P, Ecuador, 14 mo (Suarez 2006); 9) Tinigua N.P, Colombia, 12 mo (Stevenson *et al.* 2000); 10) Tinigua N.P, Colombia, 13 mo (Di Fiore *et al* in press); 11) Noel Kempff N.P., Bolivia, 11 mo (Wallace 2006); 12) Manu N.P., Peru, 21 mo (Symington 1988; Terborgh 1983); 13) This study.

breadth of plant species from which focal individuals consumed items, their diet was strongly biased in terms of the proportion of time spent feeding on certain food sources. Just 2 species comprised almost 50% of their total time spent feeding. In contrast, 86% of the recorded food species were each represented by ≤1% of total feeding time. Such heavy reliance on just a few plant species is a common pattern for communities of *Ateles* (Cant 1990; Chapman 1988; Dew 2005; Nunes 1998; Wallace 2005).

Plant resources that feature strongly in an individual's diet are not necessarily preferred because they may be selected in relation to their availability in the habitat. We found a great range in preference indices indicating that subjects strongly preferred a few taxa and strongly avoided a few others, while they consumed a large number of taxa according to availability (Table 3). The most highly preferred species by *Ateles chamek* in La Chonta was *Virola sebifera* (Myristicaceae). The species is rare in the study area and we observed *Ateles chamek* to eat its fruit only on a few occasions. *Virola* produce lipid-rich fruit that feature prominently in diets of *Ateles* spp. (Dew 2005; Russo *et al*. 2005; Stevenson *et al*. 2000; van Roosmalen 1985). *Ficus* was also highly ranked in our preference analysis, which mirrors the observed disproportionate consumption of fruit from the genus: 49% of all time spent feeding was spent in *Ficus*.

Ficus is one of the most widespread genera of tropical plants (Janzen 1979). The phenology of *Ficus* is unique because fig trees depend on species-specific symbionts (agonid wasps) for their pollination and have evolved to produce very large crops of fruit at short intervals that favor the continuous development of the symbionts (Janzen 1979). It is the combination of large fruit crops and asynchronous intrapopulation fruiting that makes fig trees important keystone resources for many tropical frugivores (Leighton and Leighton 1983; Shanahan *et al*. 2001; Terborgh 1983, 1986). In addition, figs provide a range of essential nutrients and minerals (Conklin and Wrangham 1994; O'Brien *et al*. 1998). Despite all the mentioned benefits of *Ficus*, relatively few Neotropical frugivores actually seem to prefer figs when other fruit are highly available (Milton *et al*. 1982; Shanahan *et al*. 2001). Exceptions include fig-specialist fruit bats (August 1981), and some populations of predominantly folivorous howlers that eat figs at all times of the year (*Alouatta palliata* in Panama: Milton 1980). We may need to add La Chonta's spider monkeys to this list of exceptions.

Our results clearly show that figs were a preferred food both during times when ripe fruit was plentiful in their home range and when it was scarce. Researchers have not previously observed such consistent consumption of *Ficus* by species of *Ateles*, even though *Ficus* occurs in every diet of *Ateles* studied to date (Di Fiore *et al*. in press). *Ficus* played a major role in the diet of *Ateles chamek* in 6 of the 9 mo of detailed feeding data collection (Table 4). In fact, in 3 mo *Ficus* contributed to >40% of their feeding time budget. Statistically, the availability of figs was the driving factor behind daily time spent feeding. In contrast, the average dietary contribution of *Ficus* as reported for other study communities of *Ateles* is 9% (range 0.9–29%, Table 5). The contribution of *Ficus* does not appear to be related to the diversity of species of *Ficus* included in diets (Table 5). The study in which a community of *Ateles* consumed figs at a proportion (29%) that was comparable to that seen in La Chonta, involved *Ateles geoffroyi* in Santa Rosa National Park, Costa Rica

(Chapman 1987, 1988). Heavy reliance on figs by both study communities may be related to the fact that both forests are semideciduous with marked seasonal differences in rainfall and temperature that results in longer-than-normal dry seasons (Janzen 1983; Justiniano and Fredericksen 2000). Why these aspects of forest ecology appear to coincide with higher dependence by *Ateles* on *Ficus* is as yet not understood.

The time *Ateles chamek* spent eating figs is almost equally divided between the 2 most commonly occurring species: *Ficus boliviana* (50%) and *F. trigona* (48%). Interestingly, subjects harvested the 2 species for figs at different maturity phases: 65% of the time spent eating figs of *Ficus boliviana* was on the consumption of unripe figs, while the equivalent value for *F. trigona* was only 10%. *Ficus boliviana* was the primary source of unripe fruit in general (68%). Normally, researchers do not report unripe figs as a significant food item for *Ateles* (Table 5). Singularly, Wallace (1998) reported a proportion that was very small (0.1% of total feeding time). Some of our feeding observations of unripe figs occurred when ripe figs were scarce in the home range (Fig. 6). Such periods of ripe fig scarcity were the result of synchronous fruiting pattern of the most common species of *Ficus* in the forest. Periods of ripe fig scarcity may not be annual, or even of frequent occurrence in La Chonta. Great interannual differences in phenology of *Ficus* occur (Milton 1991), and *Ficus* elsewhere in La Chonta provide ripe fruit crops continuously over the year (Fredericksen *et al*. 1999). However, we have shown that at the scale of a spider monkey community's home range, critical periods of ripe fig scarcity occur. During such periods, unripe fig crops are available (Fig. 3) because an individual tree's crop stays unripe for 3–4 times as long as it stays ripe (Norconk *et al*. 1998). Such difference in temporal availability would explain their choice of unripe figs during times of ripe fig scarcity.

Surprisingly, *Ateles chamek* also consumed unripe figs at times when ripe figs were abundant. Subjects consumed unripe figs of *Ficus boliviana* both when ripe figs were plentiful and when ripe fruit in general were highly abundant (Fig. 6). Interestingly, a similar pattern occurred in a chimpanzee (*Pan troglodytes*) community in Uganda where 1) figs and leaves of *Ficus* were constant staple foods, featuring in their diet all through the year, and 2) they harvested several of the species of *Ficus* for their unripe and ripe figs, with the former occasionally preferred (Newton-Fisher 1999).

Ficus was not the sole provider of unripe fruit. Overall, *Ateles chamek* fed on unripe fruit for 23% of their feeding time. No other study on *Ateles* has documented as many months in which unripe fruit pulp made up >5% of feeding time (Table 5). The period with the highest percentage of unripe fruit consumption time was May (45%), which fell within the long period of fruit scarcity. Researchers frequently report unripe fruit, often in combinations with leaves, as an important fallback food for spider monkeys during lean times (Iwanaga and Ferrari 2001; Milton 1993; Wallace 2005). Indeed, owing to limitations of their gut morphology and digestive abilities, spider monkeys cannot switch entirely to folivorous diet in times of fruit scarcity (Milton 1993), thereby potentially increasing their requirement for unripe fruit. However, even during months with high recorded general food availability, *Ateles chamek* spent a large amount of time eating unripe fruit and figs (July: 23% and August: 18%). At La Chonta, unripe fruit is therefore an almost continuous component of their diet, rather than a backup food resource consumed only in times of general food scarcity.

It is important to clarify the difference between unripe pulp consumption and the consumption of unripe fruit for the purpose of digesting the seeds. True seed predation is a rare phenomenon in the diets of *Ateles* (Di Fiore *et al*. in press). In their multisite comparison of seed dispersal by *Ateles*, Russo *et al*. (2005) found that on average only 3.2% of feeding observations involved seed predation (range 1.1–6.5%). They describe seeds as predated if they are ingested but not defecated intact, or if they were masticated before being swallowed. Besides spitting out the large seeds of palm fruit, *Ateles chamek* in La Chonta swallowed seeds of all fruit sources whole and passed seeds intact. They never masticated them. Even though seeds typically mature somewhat earlier than the pulp (Janson and Chapman 1999) we have no evidence as to whether seeds from unripe fruit and figs that *Ateles chamek* consumed were viable or not. If they are not viable, the action of removing immature seeds from the tree, and thus prohibiting the seeds to mature, leads to similar seed fate as in cases of true seed predation. To understand the actual impact of such seed removal on tree regeneration, researchers need to test seed viability across a range of developmental stages of unripe fruit consumed by spider monkeys.

Interannual variation in spider monkey dietary composition can be high (Chapman 1987), and admittedly our study is but a glimpse of time in the lives of this community. Given that our study period overlapped with both periods of fruit abundance and scarcity, and observed rainfall was similar to the annual averages for the forest, we assumed that our results represent the primate population’s normal patterns. Researchers regard *Ficus* as a keystone resource owing to its critical role in the ecology of tropical frugivores in times of fruit scarcity (Shanahan *et al*. 2001; Terborgh 1983, 1986). The heavy reliance on *Ficus* by La Chonta *Ateles* elevates its value from a fallback food to an important food source throughout the year. Several researchers already regard figs as an all-round important staple food for bonobos and chimpanzees (Conklin and Wrangham 1994; Newton-Fisher 1999; White 1998; Wrangham *et al*. 1993). We suggest that a similar change in appreciation of fig trees should be reached for Neotropical frugivores for which figs constitute a staple. This is important because free-standing fig trees such as *Ficus boliviana* are harvested for timber. Bolivian forests such as La Chonta are becoming more and more deficient in young and mature individuals of *Ficus boliviana* (Mostacedo and Fredericksen 1999). It is of great concern in terms of conservation to understand in what way a decline in this staple food source will affect the population of *Ateles chamek*.

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Appendix

Table 6 All food sources of *Ateles chamek* in La Chonta, showing % time spent feeding over the year from different pheno-phases. Full and partial follow days included

Family	Scientific name	Cat.[a]	% time[b]	Rank[c]	R%	U%	YL%	L%	F%	OV%	I %	Month[d]
TOTAL FOR STUDY:					59.1	23.0	10.1	2.9	4.7	0.2	0.1	
Amaranthaceae	*Chamissoa* sp.1	L	[e]	52–66	x							-
Anacardiaceae	*Spondias mombin* L.	**T**	1.94	11	1.94							3–4
Annonaceae	*Rollinia herzogii* R. E. Fries	T	0.08[e]	34–35	0.08							-
Araceae	*Monstera sp.*	E	0.03	41–42						0.03		-
Araliaceae	*Dendropanax arboreus* (L.) D. & P.	**T**	2.32	8	2.32							7–8
Araliaceae	*Didymopanax morototoni* Decne. & Planch.	**T**	0.13	27–29	0.13							8
Arecaceae	*Astrocaryum murumuru* C. Martius	**P**	0.49	20	0.49							3–5
Arecaceae	*Attalea phalerata* Mart. ex Spreng.	**P**	0.22	24	0.11					0.11		10
Arecaceae	*Bactris gasipaes* Kunth.	**P**	0.01	45–49					0.01			-
Arecaceae	*Socratea exorrhiza* H. A. Wendl.	**P**	0.57	19	0.57							cont.
Arecaceae	*Syagrus sancona* Karsten	**P**	0.09	30–33					0.09			8–2
Asclepiadaceae	*Marsdenia macrophylla* E. Fourn	L	0.15	26				0.15				-
Bignoniaceae	*Arrabidaea verrucosa* (Standl.) A.H. Gentry.	**L**	[e]	52–66			x					spor.
Bignoniaceae	*Clytostoma uleanum* Kraenzl.	**L**	0.05	37					0.05			0
Bignoniaceae	*Melloa quadrivalvis* (Jacq.) A.H. Gentry	**L**	0.93	16			0.80	0.14				0
Bignoniaceae	*Tabebuia serratifolia* (Vahl) G. Nicholson	**T**	[e]	52–66				x				0
Bignoniaceae	*Tanaecium nocturnum* Bureau & K. Schum.	**L**	0.02	43–44				0.02				0
Boraginaceae	*Cordia alliodora* (Ruiz & Pavón) Oken	**T**	[e]	52–66	x							11–12
Caesalpiniaceae	*Caesalpinia pluviosa* DC.	T	0.01	45–49			0.01					-
Caricaceae	*Jacaratia spinosa* (Aubl.) A. DC.	**T**	1.27	14	0.60	0.11	0.04	0.17	0.35	0.01		11–5
Cecropiaceae	*Cecropia concolor* Willd.	**T**	0.02[e]	43–44	0.02							2–4 7–8
Chrysobalanaceae	*Hirtella triandra* Sw.	T	0.09	30–33	0.09							-
Combretaeae	*Terminalia oblonga* (Ruiz & Pavón) Steudel	T	0.09	30–33			0.08	0.00				-
Convolvulaeae	*Merremia cf. ternifolia* Pittier.	L	0.01	45–49			0.01					-
Dioscoreaceae	*Dioscorea anthogene*	L	0.09	30–33	0.05		0.02	0.02				-

Euphorbiaceae	*Hura crepitans* L.	**T**	[e]	52–66		x					cont.
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	**T**	1.46	12	1.44	0.02					2–3
Fabaceae	*Machaerium oblongifolium* Vogel	**L**	1.05	15			1.05				0
Lecythidaceae	*Cariniana ianeirensis* R. Knuth	T	[e]	52–66		x					-
Malvaceae	*Ceiba pentandra* (L.) P. Gaertner	**T**	0.20	25			0.20				0
Malvaceae	*Ceiba speciosa* St. Hilaire	**T**	<0.01	50–51			0.00				5–10
Melliceae	*Guarea guidonia* (L.) Sleumer	T	[e]	52–66	x						-
Mimosaceae	*Inga edulis* Mart.	**T**	1.35	13	1.35						2–4
Moraceae	*Batocarpus amazonicus* (Ducke) Fosb.	**T**	2.28	9	x		2.26	0.01			11
Moraceae	*Brosimium guadichaudii* Trécul	**T**	0.04	38–40			0.04				10–11
Moraceae	*Ficus boliviana* C.C. Berg	**T**	28.59	1	8.56	15.6	4.38	0.01		0.00	spor.
Moraceae	*Ficus eximia* Schott	**T**	0.45	21	0.31	0.14				0.00	-
Moraceae	*Ficus gomelleira* Kunth & Bouché	**T**	0.04[e]	38–40		0.04					-
Moraceae	*Ficus pertusa* L. f.	**T**	0.13	27–29	0.11	0.02					spor.
Moraceae	*Ficus sp.*	**T**	[e]	52–66	x						0
Moraceae	*Ficus trigona* L. f.	**T**	20.31	2	17.8	2.00	0.47				spor.
Moraceae	*Pseudolmedia laevis* J. F. Macbride	**T**	9.36	4	2.98	2.23	0.12	0.01	4.02		8–11
Myristicaceae	*Virola sebifera* Aublet	**T**	0.44	22	0.44						5, 8
Myrtaceae	*Myrciaria* sp.	**T**	10.30	3	10.3						2–8
Nyctaginaceae	*Neea cf. steimbachii* Heimerl	T	[e]	52–66			x				-
Quiinaceae	*Quiina florida* Tul.	**T**	[e]	52–66	x						0
Rubiaceae	*Alibertia verrucosa* S. Moore	**T**	0.03	41–42	0.03						10–2
Rubiaceae	*Calycophyllum spruceanum* (Benth.)	T	[e]	52–66						x	-
Rutaceae	*Zanthoxylon rhoifolium* Lam.	T	0.01	45–49		0.01					-
Sapindaceae	*Paullinia elegans* Cambess.	**L**	0.59	18	0.59						3–4
Sapindaceae	*Talisia esculenta* (Cambess.) Radlk.	T	0.04	38–40	0.04						-
Sapotaceae	*Pouteria macrophylla* (Lam.) Eyma	**T**	[e]	52–66	x						3, 8, 12
Sapotaceae	*Pouteria nemorosa* Baehni	**T**	4.08	5	1.31	2.73				0.05	2–3
Sterculiaceae	*Guazuma ulmifolia* Lam.	**T**	3.57	7	3.57						6–10
Styraceae	*Styrax tessmannii* Perkins	**T**	[e]	52–66	x						5, 8
Tilliaceae	*Heliocarpus americanus* L.	T	2.16	10			0.15	2.02			-
Ulmaceae	*Ampelocera ruizii* Klotzsch	**T**	0.30	23			0.16	0.03	0.11		10–12
Ulmaceae	*Celtis iguanea* (Jacq.) Sarg.	**L**	3.84	6	3.84						3–6
Urticaceae	*Urera baccifera* (L.) Gaudich.	T	0.13	27–29			0.03	0.10			-

Table 6 (continued)

Family	Scientific name	Cat.[a]	% time[b]	Rank[c]	R%	U%	YL%	L%	F%	OV%	I %	Month[d]
Vitaceae	*Vitaceae sp. 1*	**L**	0.01	45–49						0.01		12
	Unidentified plant (1 sp)	T	<0.01	50–51				0.00				
	Unidentified lianas (4 spp)	**L**	0.65	17		0.02	0.27	0.24	0.12			
	Unidentified insect	I	0.08	34–35							0.08	
	unidentified epiphyte (1 sp)	E	[e]	52–66	x							
	Unid. caterpillars in *Terminalia oblonga*	I	[e]	52–66							x	
	Unid. arboreal termite mound	I	0.06	36							0.06	

Full and partial follow days are included.

R = Ripe fruit; U = unripe fruit pulp; YL = young leaves; L = leaves; F = flowers; OV = other vegetative material; I = insects. Percentages of these items are of total feeding time in study.

[a] Category of food source: T = tree; L = liana; P = palm; E = epiphyte; I = insect. Bold letters indicate inclusion of species in respective phenology index (see Methods).

[b] Percentage of total feeding time in study.

[c] Ranking of contribution in terms of %time.

[d] Month(s) when species produced ripe fruit (spor. = sporadic; cont. = continuous; 0 = no fruit during study; - = not included in survey; 1 = January; 2 = February, etc).

[e] Primarily observations made during habituation; therefore no or only little detailed time information available. x = depicts which type of item was consumed of the species.

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