

# Lianas as a food resource for brown howlers (*Alouatta guariba*) and southern muriquis (*Brachyteles arachnoides*) in a forest fragment

M. M. Martins

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## Abstract

*Lianas as a food resource for brown howlers (Alouatta guariba) and southern muriquis (Brachyteles arachnoides) in a forest fragment.*— Lianas, woody vines, are abundant and diverse in tropical forests, but their relative contribution as a source of food for herbivores has been neglected. I compared feeding rates on lianas and trees of two sympatric primates, *A. guariba* and *B. arachnoides*, in Southeastern Brazil. Availability of liana foods was gathered in parallel with primate behavioral data collection. Liana represented 33.9% and 27.3% of food sources for *A. guariba* and *B. arachnoides*, respectively. Foods coming from trees, rather than from lianas, were significantly more consumed by *B. arachnoides*. However, both species took advantage of the continuously renewable and ephemeral food resources provided by liana. Availability of liana flowers correlated positively with *A. guariba* feeding proportions. The nutritional supply provided by lianas is apparently beneficial, or at least unharmed, but experiments comparing primate choices in forests with different liana abundances will help to shed light on their possible negative effect on communities.

Key words: Lianas, Primates, Diet, Forest fragmentation.

## Resumen

*Las lianas como recurso alimentario para el mono aullador (Alouatta guariba) y el muriqui meridional (Brachyteles arachnoides) en un área forestal.*— Las lianas (enredaderas leñosas) son muy abundantes y presentan una gran diversidad en las selvas tropicales; sin embargo no se ha tenido en cuenta su contribución relativa como fuente de alimento para los herbívoros. En el presente estudio se comparan las tasas de consumo a base de lianas y de árboles de dos especies de primates simpátricas, *A. guariba* y *B. arachnoides*, en el sudeste de Brasil. Se llevó a cabo un estudio de la disponibilidad de lianas como recurso alimentario, paralelamente a la recolección de datos sobre la conducta de los primates. Las lianas representaron el 33,9% y el 27,3% de los recursos de *A. guariba* y *B. arachnoides*, respectivamente. El consumo de alimentos procedentes de los árboles, en vez de las lianas, fue significativamente mayor en *B. arachnoides*. Sin embargo, ambas especies aprovechaban los recursos continuamente renovables y efímeros que proporcionaban las lianas. La disponibilidad de las flores de las lianas se correlacionaba positivamente con las proporciones de consumo por parte de *A. guariba*. Aparentemente, el suministro alimentario proporcionado por las lianas es beneficioso o al menos inocuo, pero futuros experimentos en que se compare la elección de los primates en selvas con distintas abundancias de lianas ayudarán a aclarar su posible efecto negativo sobre las comunidades.

Palabras clave: Lianas, Primates, Dieta, Fragmentación forestal.

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Milene Moura Martins, Post-graduate Program, Biological Science (Zoology), Depto. de Zoologia, Inst. de Biociências, Univ. de São Paulo (USP), CP 11461, CEP 05422-970, São Paulo, SP, Brazil.

Current address: Lab. de Biodiversidade Molecular e Citogenética, Depto. de Genética e Evolução, Univ. Federal de São Carlos (UFSCar), São Carlos, SP, Brazil. E-mail: [milenemartins@terra.com.br](mailto:milenemartins@terra.com.br)

## Introduction

Lianas are woody climbing vines (*sensus* Gentry, 1991) that rely on other plants for support. They encompass 25% of species diversity in tropical systems (Schnitzer & Bongers, 2002). There is a growing body of evidence pointing to an increase in abundance of lianas in forests (Phillips et al., 2002; Wright et al., 2004; Swaine & Grace, 2007). Liana diversity and abundance has been shown to increase following disturbance in comparisons between forest edges and interiors (Oliveira-Filho et al., 1997; Laurance et al., 2001) and between secondary and old growth forests (DeWalt et al., 2000). By producing many rooting stems, lianas are able to rapidly colonize disturbed areas, thereby increasing their chances of survival (Schnitzer & Bongers, 2002).

It has been suggested that lianas are important to forest-dwelling animals because they provide food resources and pathways (Emmons & Gentry, 1983). However, investigations reporting on the relative contribution of lianas as a food source in comparison to other life forms are lacking. Because Neotropical primates have undergone a broad adaptive radiation towards arboreal lifestyle and folivorous / frugivorous habits (Cowlshaw & Dunbar, 2000), it would be expected that lianas would play a substantial role in their feeding preferences. The protein/fiber ratio and tannin content, for instance, are determinants of food choices of predominantly folivorous primates (Milton, 1979; Ganzhorn, 1992). As they rapidly colonize forest gaps, lianas might be more effective providers of young leaves with favorable protein/fiber ratio and lower concentration of digestion-inhibitors when compared to trees. Also, since the production of foods offered by lianas fluctuates in a seasonal pattern (Putz & Windsor, 1987; Opler et al., 1991; Morellato & Leitão-Filho, 1996) and lianas reproduce during periods unfavorable to trees (Morellato & Leitão-Filho, 1996), it might be advantageous for primates to rely on food items provided by woody climbers. Whether higher rates of consumption of liana products lead to an increase in primate population size is an unresolved question because of the scarcity of data. One of the few studies on the effects of liana abundance, carried out in African forests, found evidence of a positive association between *Colobus guereza* densities and lianas in the larger size classes (Preece, 2006).

The brown howler (*Alouatta guariba*) and the southern miqui (*Brachyteles arachnoides*) are primate species of the Atelidae family (Groves, 2001) living sympatrically in some Atlantic Forest fragments in Southeastern Brazil. The contribution of lianas to the overall diet of these two species is rarely mentioned in studies of their feeding habits. Thus, current available information is mainly anecdotal. After finding that 41% of leaves consumed by a group of *A. guariba* came from lianas, Chiarello (1994) suggested that habitat disturbance resulted in the proliferation of lianas, which was beneficial for howlers. Mendes (1989) reported that liana leaves represented 11.3% of the leaf diet of another howler group. *B. arachnoides* was observed feeding on leaves of two liana species

(Torres de Assumpção, 1983). Woody vines made up 37–47% of feeding time of a *B. arachnoides* group studied by Milton (1984). Data on other congeneric species is also scanty: the liana *Forsteronia glabrescens* was the second most consumed species by *A. caraya* in Northern Argentina (Zunino, 1989). In a three-month study, Fonseca (1985) recorded 14% of liana leaves in the diet of *B. hypoxanthus*. Asensio et al. (2007) suggested that the high population density and increased rate of depletion of primary food sources are forcing groups of howlers in a Mexican forest fragment to forage on alternative resources, such as vines, lianas, shrubs and herbs.

Howlers and miquis differ in terms of locomotion. While howlers walk in a predominantly quadrupedal, slow-motion fashion (Mendel, 1976), miquis practice brachiation, hanging by their long arms and tail to swing among crowns of adjacent trees. Miquis are therefore able to cover a larger area in comparison to howlers, and within the same period of time they can visit a higher number of widely dispersed food patches, such as flowering and fruiting trees. I investigated the feeding ecology of sympatric groups of *A. guariba* and *B. arachnoides* in a forest patch in Southeastern Brazil, where they occur at densities of 27 and 35 ind/km<sup>2</sup>, respectively (Martins, 2005). I compared the species in terms of feeding on resources available from trees and lianas. I also compared them for their intake of liana leaves, flowers and fruit on a monthly basis. I predicted that: 1) because miquis move faster from one resource patch to another than howlers, they would feed less on lianas, and 2) food resources provided by lianas would be consumed by both species of primates in accordance with their availability.

## Methods

### Study site

The study was carried out at the Fazenda Barreiro Rico (22° 41' S, 48° 06' W), a cattle ranch located in the eastern range of the central Plateau, in the state of São Paulo, Southeastern Brazil. Low topographic relief and poor, sandy soils characterize the central Plateau region, which is bordered by the humid Atlantic Forest in the coastal eastern range and the Cerrado domain to the west. I collected data in a 1,450 ha semideciduous forest fragment. Seventy-six species of trees and 21 species of vines were recorded at the site (Assumpção et al., 1982). There is a profusion of canopy gaps and considerable abundance of lianas, as 32.8% of 400 phenologically censused trees bore lianas (unpubl. data). This probably resulted from many decades of selective logging in this patch. Large, emergent trees still remain in old, regenerated logged areas. The predominant climate is mesothermic. Mean annual rainfall is 1,284.5 mm (data from a local climatological station), with rains falling mostly between January and March. A moderate to severe drought (< 70 mm of monthly rainfall) occurs from April to September.

### Study groups

Two groups of *A. guariba* and *B. arachnoides* (one species each) were habituated to the presence of observers before data collection. These groups were randomly selected in respect to the proportion of trees infested by lianas in their ranging areas. Like other groups observed in the population survey, the ranging area of study groups comprised regions with higher and lower visibility on account of lianas. The group of *A. guariba* comprised six members: one adult male, one sub-adult male, two adult females, a juvenile male, and an infant male. The non-cohesive, ever-changing social units of *B. arachnoides* averaged  $3.25 \pm 1.65$  individuals. While the members of the *A. guariba* group were easily recognized by their natural markings, only 13 adult females and dependent young *B. arachnoides* could be reliably identified. The miquiqui group probably contained 25 to 30 members, a group size estimated by adding the total number of adult females, their offspring, and the largest clump (11) recorded for males on an incomplete day of observation.

### Sampling of feeding behavior

From June 2001 to May 2002, observations were carried out on four to five consecutive days per month (from dawn to dusk) for *A. guariba* and *B. arachnoides* groups, totaling 40 and 38 full days, respectively. During this year-long period, I collected 2,038 feeding records for *A. guariba* and 2,122 for *B. arachnoides*. To collect feeding data, I used an instantaneous scan sampling technique: scans lasted one minute followed by an interval of five minutes. The behavior of all the animals that came into view was assigned to one of the following categories: moving, resting, eating, or interacting socially. Whenever individuals were eating, I recorded whether the food source was leaves, flowers, or fruits. I also recorded whether the food source had been obtained from a liana or a tree. Although individual recognition of *B. arachnoides* was constrained by the absence of natural markings, I took care about not recording the same animal twice per observation session.

### Phenology of resources

I selected 131 bunches of lianas that were hanging on tree branches. I considered a strict definition of liana, *i.e.*, climbers that germinate on the forest floor and produce true wood (see Gerwing et al., 2006). Due to the difficulty of collecting and identifying lianas, each bunch was considered as a single sampling unit, regardless of how many and which species it was composed of. If more than one bunch was being supported by the tree, one of them was randomly selected. The bunch was sampled regardless of whether the lianas climbed the tree directly or came from the crown of an adjacent tree. These bunches of lianas were carefully observed at three-weekly intervals in parallel with sampling of the behavior. Abundance of

resources (leaves, flowers and fruits) was evaluated using a scale of degree of availability that ranged from 0 to 4 (0 = total absence, 4 = full crown). To avoid the subjectivity associated with the classification, I did not distinguish between mature and young leaves, nor between ripe and unripe fruits. An index of availability (IA) was calculated monthly for each food resource using the formula:

$$IA = \frac{\text{Sum of degrees of availability}}{\text{Total degree of availability}} \times 100$$

Percentages of monthly IA for all three food items were calculated. Voucher specimens were collected whenever possible and deposited at the Herbarium of the University of São Paulo. Identification, whenever possible, was carried out to the species level.

### Data analyses

Mean annual and monthly percentages of food resources in the diet of the primates were calculated using only the feeding records gathered on complete days of observation. I calculated daily proportions of food resources that the primates collected from each source (trees or lianas) by dividing the number of records for that source by the total daily number of feeding records. The same procedure was carried out to calculate the daily proportions of leaves, flowers, and fruits that primates collected from lianas. Feeding proportions for a given month were obtained by dividing the sum of proportions by the number of the full days of observation in that month.

Differences between the species relative to the daily proportions of feeding on resources provided by trees and lianas was tested by two-way ANOVA. The data set was previously tested for homogeneity of variances by means of Levene's test (Zar, 1999). Interactions between monthly proportions of feeding on leaves, flowers, and fruits gathered from lianas and availability indexes were tested by Spearman rank correlation test. The software STATISTICA v.5.0 was used to carry out the tests, and the significance level was set at 0.05.

## **Results**

Resources from liana represented 33.9% (691/2,038) of total feeding records for howlers and 27.3% (579/2,122) for miquiquis over the 12 month study period. *A. guariba* and *B. arachnoides* fed on at least 12 and 10 species of lianas, respectively. Taxonomic determination was possible for only nine species (table 1), mostly because plant specimens grew in inaccessible places high in the tree canopies.

The significant difference between sources (trees and lianas) in the diet of the primates ( $F = 9.95$ ;  $P = 0.00$ ) along with the significant interaction ( $F = 9.73$ ;  $P = 0.02$ ) between species and sources indicated that foods coming from trees are considerably more consumed by *B. arachnoides* when compared to foods coming from lianas (fig. 1).

Table 1. Liana species in the diet of *Alouatta guariba* (Ag) and *Brachyteles arachnoides* (Ba): C. Consumer.

Tabla 1. Especies de liana de las dietas de *Alouatta guariba* (Ag) y *Brachyteles arachnoides* (Ba). C. Consumidor.

Species	Family	C
<i>Adenocalymma</i> sp.	Bignoniaceae	Ag
<i>Diclidanthera</i> sp.	Polygalaceae	Ag, Ba
<i>Dolichandra unguis-cati</i>	Bignoniaceae	Ba
<i>Fridericia samydoides</i>	Bignoniaceae	Ag
<i>Lundia obliqua</i>	Bignoniaceae	Ba
<i>Pereskia aculeata</i>	Cactaceae	Ag, Ba
<i>Serjania</i> sp.	Sapindaceae	Ag
<i>Stizophyllum riparium</i>	Bignoniaceae	Ba
<i>Tanaecium selloi</i>	Bignoniaceae	Ag

Difference between the species in terms of relative contribution of the two sources was not significant ( $F = 0.0$ ;  $P = 1.0$ ).

Availability of liana leaves followed a regular pattern (fig. 2A), as illustrated by the proximity of the

minimum and maximum IA values (74.8 and 85.1). Availability of flowers and fruits followed seasonal patterns (figs. 2C, 2E). Flower production peaked at the beginning of the wet season (September), and availability values were high throughout the first months of the season (October and November). There was a small, second peak in May. High abundance (8–9%) of liana fruits occurred in November–December, dropping sharply after that (fig. 2E). Fruit production remained below 4% during the rest of the year.

The percentage of total feeding records for a given month varied widely among food items consumed by each species (fig. 2). While leaves were the staple food item throughout the year both for howlers and muriquis, flowers and fruits were consumed much less or not consumed at all. On a monthly basis, the percentage of liana leaves in the howlers' diet varied widely in comparison to that in the muriquis' diet. This food item composed a minimum of 7% of the diet of *A. guariba*, but peaked at 49% in August (fig. 2A). Unlike howlers, the maximum leaf consumption of muriquis remained at intermediate levels, such as 28% (fig. 2E). Liana leaves were consumed less by *B. arachnoides* from January to March, following the overall tendency of reduced leaf consumption, probably as a response to higher fruit availability during the wet season. The highest percentages of liana flowers in the diet of *A. guariba* and *B. arachnoides* were 23% and 17%, recorded in February and September, respectively (figs. 2C, 2D). The explosive consumption shown by howlers in February, in discordance with availability, would

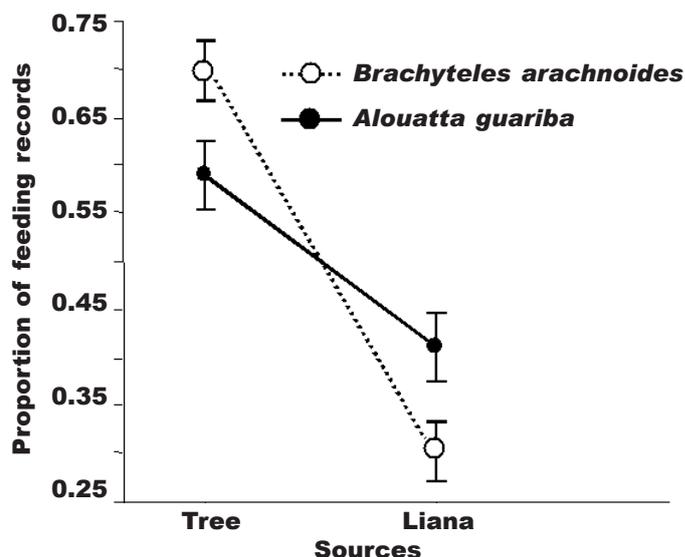


Fig. 1. Mean annual proportions of feeding records on tree and liana by *Alouatta guariba* and *Brachyteles arachnoides*.

Fig. 1. Proporciones anuales medias de los registros alimentarios de *Alouatta guariba* y *Brachyteles arachnoides* de árboles y lianas.

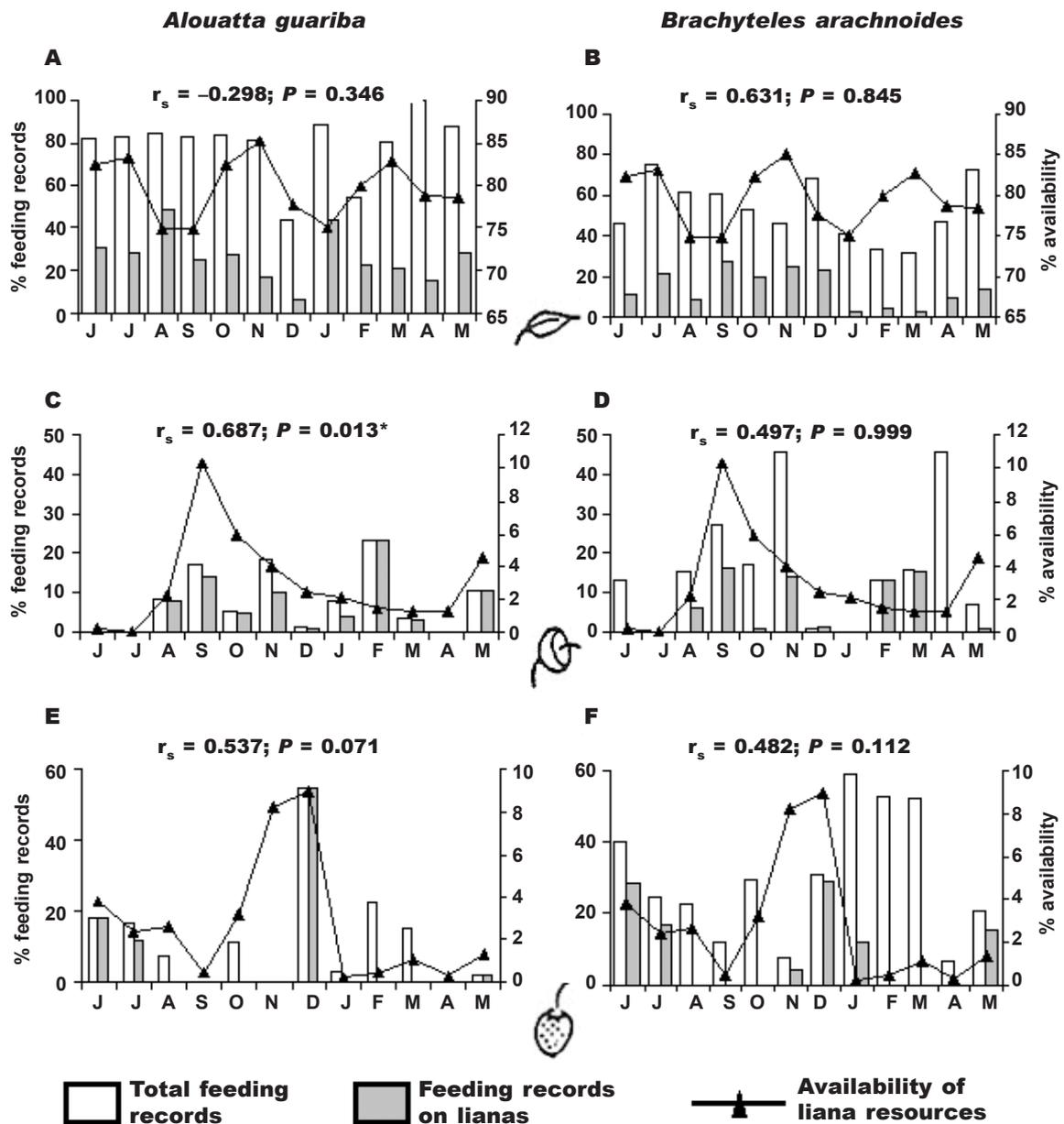


Fig. 2. Monthly percentage of feeding records by *Alouatta guariba* and *Brachyteles arachnoides* and percentage of availability index of leaves, flowers, and fruits of lianas. Spearman correlations are between monthly proportions of feeding records on liana foods and availability indexes of lianas: \* Significant at 0.05.

Fig. 2. Porcentaje mensual de registros alimentarios de *Alouatta guariba* y *Brachyteles arachnoides* e índice del porcentaje de disponibilidad de hojas, flores y frutos de las lianas. Las correlaciones de Spearman se aplican entre la proporciones mensuales de registros de consumo de alimentos de las lianas y los índices de disponibilidad de las lianas: \* Significativo en 0,05.

have led to a negative relationship had February not been an exception to the rule. On one day in this month, the group twice visited an unidentified species of flowering liana and devoured almost all the flowers. Even so, the percentage of consump-

tion varied significantly in accordance with availability (fig. 2C). *A. guariba* showed an opportunistic behavior during the two blooms of liana flowers, in the early wet and in the dry season. In contrast, *B. arachnoides* fed substantially on liana flowers during

the first peak of availability in September, but not during the second flowering in May (fig. 2D). Feeding on liana fruits peaked in December (55%) for *A. guariba* and peaked twice (June and December, both 29%) for *B. arachnoides*. (figs. 2E, 2F). The primate species shared a seasonal pattern of fruit consumption: June–July and December. In these periods both primate species mainly consumed the fruits of two liana species: *Pereskia aculeata* in the former period and *Diclidanthera* sp. in the latter period. Both of these plant species were abundant and easily recognized by the unique morphology and color of their fruit. The yellow-colored fruits of *Pereskia aculeata* bore spines on the epicarp, but these did not seem to be a deterrent to the animals. Fruits of *Diclidanthera* sp. were juicy, violet drupes. The monthly patterns of flower and fruit feeding by the two primate species revealed opposite phases: higher relative feeding rates on flowers were recorded during periods in which fruits were eaten less or not eaten at all and vice-versa. Only the availability of liana flowers presented a positive significant correlation with consumption by howlers.

## Discussion

The mean annual percentage of lianas in the diet of *A. guariba* (27%) is similar to that of *B. arachnoides* (33%). However, on a daily basis, the latter rely much more on resources from trees than from lianas. The greater quantity of trees in the muriquis' diet matches expectations as they can reach widely disperse areas by brachiation. It is not yet known whether muriquis would replace resources from trees with those from lianas if the latter became more abundant as the result of habitat disturbance. Lianas may outcompete trees through the combined effects of shading and negative impact on sapling growth (Putz, 1984; Schnitzer et al., 2005). If muriquis are unable to make such a replacement due to constraints of dietary requirements changes in their feeding rates would be expected in the long-term. It appears that *A. guariba* would consume a greater amount of lianas the greater their abundance, but this would likely not be the case of *B. arachnoides* unless the tree resources they rely on have their growth, fecundity and/or recruitment rates negatively affected by lianas.

On a monthly basis, liana resources were present in the diets of both *A. guariba* and *B. arachnoides*. It is known that atelines are flexible in terms of food choice (Chapman, 1987) and high dietary flexibility of both ateline species was evident in this study, illustrated by the consumption of resources from plants with different growth habits. Food choices also showed a temporal pattern of flexibility. The monthly fluctuation of flower and fruit availability favored the shift from one resource to another in consecutive months. Fleshy fruits supply non-structural, easily digested carbohydrates, the major components of the pulp (Waterman, 1984). Flowers eaten by primates provide protein and minerals (Castellanos & Chanin, 1996; Silver et al., 2000). By shifting between these

foods, primates can fulfill their requirements at any time of the year.

With the exception of flower consumption by *A. guariba*, no significant correlations were found between the availability of food resources and the monthly proportion of feeding records for either *A. guariba* or *B. arachnoides*. This finding suggests that attributes other than abundance might govern consumption. The howlers' recognized strategy of maximizing protein intake (Milton, 1979) might have favored their reliance on a patchily distributed resource such as flowers. Flowering trees are perhaps distributed further apart from each other, on average, than lianas, and this would limit the consumption of their flowers by *A. guariba*, a species that moves in a quadrupedal, slow-motion fashion. The same limitation would be expected for fruit, since they do not fulfill the howlers' high protein requirements as well as flowers (and leaves) do. In the case of *B. arachnoides*, however, brachiation would not prevent them from opportunistically exploiting liana flowers. Differential nutritional demands and abilities to deal with secondary compounds possibly underlie the distinct findings for howlers and muriquis. However, there may be other explanations. Researchers have failed to find correlations between consumption by primates and availability of food resources (e.g. Chapman, 1987; Maisels et al., 1994; Peres, 1994; Stoner, 1996; Heiduck, 1997; Kaplin et al., 1998). It seems that whenever the pool of surveyed plants harbors few individuals of the species consumed, the temporal variability in the abundance of these species' resources remains hidden within the overall pattern. Indeed, this may be the case for liana species in the present study. Here, a bunch composed of perhaps two or more species, rather than a single species as usually carried out in tree phenological assessments, was selected as a sample unit. Thus, it is hard to tell whether liana species preferred by howlers and muriquis were poorly represented in the phenological sample, except for those bearing flowers and fruits with specific traits as mentioned above.

It is clear that lianas play an important role in the feeding patterns of howlers and muriquis at the present study site. This may be the result of two environmental factors, rainfall and forest disturbance, either alone or in combination. A high abundance of liana has been reported in areas of Ghana, Africa, where the rainfall is low (Swaine & Grace, 2007) and also in fragmented forests or those woodlots where timber harvesting has prevailed for years (DeWalt et al., 2000). The study site receives less than 1,300 mm of rainfall annually. Moreover, selective logging has been carried out for decades at Barreiro Rico, although rates are currently lower. Howlers and muriquis take advantage of continuously renewable (leaves) and ephemeral (flowers and fruits) liana resources. This plant group may be contributing to the growth of populations, because both species present moderate population density at the study site. Whether food items from liana have been continuously increasing in the diet of *A. guariba*

and *B. arachnoides* at the study site as a response to liana abundance is difficult to know, given the lack of long-term monitoring of their feeding choices. Although the food supplied by lianas is apparently beneficial, or at least unharmed in the setting of the mesic forest and the disturbed nature of the study site, experiments comparing primate choices in forests with different rates of liana infestation would help to shed light on the possible negative effects of such consumption in these communities.

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### References

- Asensio, N., Cristobal-Azkarate, J., Dias, P. A. D., Vea, J. J. & Rodríguez-Luna, E., 2007. Foraging habitats of *Alouatta palliata mexicana* in three forest fragments. *Folia Primatologica*, 78: 141–153.
- Assumpção, C. T., Leitão-Filho, H. F. & Cesar, O., 1982. Descrição das matas da Fazenda Barreiro Rico, Estado de São Paulo. *Revista Brasileira de Botânica*, 5: 53–66.
- Castellanos, H. G. & Chanin, P., 1993. Seasonal differences in food choice and patch preference of long-haired spider monkeys (*Ateles belzebuth*). In: *Adaptive Radiations of Neotropical Primates*: 451–466 (M. A. Norconk, A. L. Rosenberger & P. A. Garber, Eds.). Plenum Press, New York.
- Chapman, C. A., 1987. Flexibility in the diets of three species of Costa Rica primates. *Folia Primatologica*, 49: 90–105.
- Chiarello, A. G., 1994. Diet of the brown howler monkey *Alouatta fusca* in a semi-deciduous forest fragment of southeastern Brazil. *Primates*, 35(1): 25–34.
- Cowlishaw, G. & Dunbar, R. I. M., 2000. *Primate Conservation Biology*. Univ. of Chicago Press, Chicago.
- DeWalt, S. J., Schnitzer, S. A. & Denslow, J. S., 2000. Density and diversity of lianas along a chronosequence in central Panamanian lowland forest. *Journal of Tropical Ecology*, 16: 1–9.
- Emmons, L. H. & Gentry, A. H., 1983. Tropical forest structure and the distribution of gliding and prehensile tailed vertebrates. *The American Naturalist*, 121: 513–524.
- Fonseca, G. A. B., 1985. Observations on the ecology of the miqui (*Brachyteles arachnoides* E. Geoffroy 1806): Implications for its conservation. *Primate Conservation*, 5: 48–52.
- Ganzhorn, J. U., 1992. Leaf chemistry and the biomass of folivorous primates in tropical forests. *Oecologia*, 91: 540–547.
- Gentry, A. H., 1991. The distribution and evolution of climbing plants. In: *The biology of vines*: 3–52 (F. E. Putz & H. A. Mooney, Eds.). Cambridge Univ. Press, Cambridge.
- Gerwing, J. J., Schnitzer, S. A., Burnham, R. J., Bongers, F., Chave, J., DeWalt, S. J., Ewango, C. E. N., Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup, D. R., Putz, F. E. & Thomas, D. W., 2006. A standard protocol for liana censuses. *Biotropica*, 38(2): 256–261.
- Groves, C. P., 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington.
- Heiduck, S., 1997. Food choice in masked titi monkeys (*Callicebus personatus melanochir*): Selectivity or opportunism? *International Journal of Primatology*, 18(4): 487–502.
- Kaplin, B. A., Munyaligoga, V. & Moermond, T. C., 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica*, 30(1): 56–71.
- Laurance, W. F., Pérez-Salicrup, D., Delamônica, P., Fearnside, P. M., D'Angelo, S., Jerzolinski, A., Pohl, L. & Lovejoy, T. E., 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*, 82: 105–116.
- Maisels, F., Gautier-Hion, A. & Gautier, J. P., 1994. Diets of two sympatric colobines in Zaire: More evidence on seed-eating in forests on poor soils. *International Journal of Primatology*, 15(5): 681–701.
- Martins, M. M., 2005. Density of primates in four semi-deciduous forest fragments of São Paulo, Brazil. *Biodiversity and Conservation*, 14(10): 2321–2329.
- Mendel, F., 1976. Postural and locomotor behavior of *Alouatta palliata* on various substrates. *Folia Primatologica*, 26: 36–53.
- Mendes, S. L., 1989. Estudo ecológico de *Alouatta fusca* (Primates: Cebidae) na Estação Biológica de Caratinga, MG. *Revista Nordestina de Biologia*, 6: 71–104.
- Milton, K., 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, 114: 362–378.
- 1984. Habitat, diet, and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroy, 1806). *International Journal of Primatology*, 5(5): 491–513.
- Morellato, L. P. C. & Leitão-Filho, H. F., 1996. Reproductive phenology of climbers in a southeastern Brazilian forest. *Biotropica*, 28(2): 180–191.
- Oliveira-Filho, A. T., De Mello, J. M. & Scolforo, J. R. S., 1997. Effects of past disturbance and edges on three community structure and dynamics within a fragment of tropical semideciduous forest in south-eastern Brazil over a five-year period (1987–1992). *Plant Ecology*, 131: 45–66.

- Opler, P. A., Baker, H. G. & Frankie, G. W., 1991. Seasonality of climber communities: a review and example from Costa Rica dry forest. In: *The biology of vines*: 377–392 (F. E. Putz & H. A. Mooney, Eds.). Cambridge Univ. Press, Cambridge.
- Peres, C. A., 1994. Primate responses to phenological changes in an Amazonian terra firme forest. *Biotropica*, 26(1): 98–112.
- Phillips, O. L., Martinez, R. V., Arroyo, L., Baker, T. R., Killeen, T., Lewis, S. L., Malhi, Y., Mendonza, A. M., Neill, D., Vargas, P. N., Alexiades, M., Ceron, C., Fiore, A. D., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vincent, B., 2002. Increasing dominance of large lianas in Amazonian forests. *Nature*, 418: 770–774.
- Preece, G. A., 2006. Factors influencing variation in the population densities of *Colobus guereza* within selectively logged forest at the Budongo Forest Reserve: the importance of lianas during a subsistence diet. In: *Primates of Western Uganda*: 23–43 (N. E. Newton–Fisher, H. Notman, J. D. Paterson, V. Reynolds, Eds.). Springer, New York.
- Putz, F. E., 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 65(6): 1713–1724.
- Putz, F. E. & Windsor, D. M., 1987. Liana phenology on Barro Colorado Island, Panama. *Biotropica*, 19(4): 334–341.
- Schnitzer, S. A. & Bongers, F., 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*, 17(5): 223–230.
- Schnitzer, S. A., Kuzee, M. E. & Bongers, F., 2005. Disentangling above– and below–ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, 93: 1115–1125.
- Silver, S. C., Ostro, L. E. T., Yeager, C. P. & Dierenfeld, E. S., 2000. Phytochemical and mineral components of foods consumed by black howler monkeys (*Alouatta pigra*) at two sites in Belize. *Zoo Biology*, 19: 95–109.
- Stoner, K. E., 1996. Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *International Journal of Primatology*, 17(1): 1–30.
- Swaine, M. D. & Grace, J., 2007. Lianas may be favoured by low rainfall: evidence from Ghana. *Plant Ecology*, 192(2): 271–276.
- Torres de Assumpção, C., 1983. Ecological and behavioral information on *Brachyteles arachnoides*. *Primates*, 24(4): 584–593.
- Waterman, P. G., 1984. Food acquisition and processing as a function of plant chemistry. In: *Food Acquisition and Processing in Primates*: 177–211 (D. Chivers, B. A. Wood & A. Bilsborough, Eds.). Plenum Press, New York.
- Wright, S. J., Calderón, O., Hernández, A. & Paton, S., 2004. Are lianas increasing in importance in tropical forests? A 17–year record from Barro Colorado Island, Panama. *Ecology*, 85: 484–489.
- Zar, J. H., 1999. *Biostatistical Analysis*. 4th edition. Upper Saddle River, Prentice Hall.
- Zunino, G. E., 1989. Habitat, dieta y actividad del mono aullador negro (*Alouatta caraya*) en el noreste de la Argentina. *Boletín Latinoamericano de Primatología*, 1: 74–97.