



# Increased folivory in brown spider monkeys *Ateles hybridus* living in a fragmented forest in Colombia

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**ABSTRACT:** Brown spider monkeys *Ateles hybridus* are one of the most threatened primates in the Neotropics. Most of the remaining populations of this species already live either in forest fragments or in areas that face imminent anthropogenic disturbance. Understanding how these animals cope with the challenge of living in small fragments, while at the same time being a large, frugivorous mammal is crucial to design effective conservation and management strategies. We studied the diet of wild *A. hybridus* and measured forest productivity in a small (~65 ha) fragment in the Magdalena Region of northern Colombia over a period of 26 mo. Spider monkeys at this site spent far less time feeding on fruits than reported in previous studies of *Ateles* spp. living in less fragmented sites. Moreover, we registered a high consumption of leaves in every month (on average 37% of their feeding time) as well as the consistent inclusion of decayed wood in the diet. *Ficus* trees can be considered staple feeding items, as they were present in high proportions in the monkeys' diet throughout the study. Although wild populations of spider monkeys can have flexible diets that include large proportions of leaves over long periods of time, they may also be exposed to a suboptimal diet which may have negative implications for their reproduction and well-being in the long run, further compromising the viability of wild populations living in disturbed habitats.

**KEY WORDS:** Behavioral flexibility · *Ficus* · Habitat fragmentation · Leaf consumption

## INTRODUCTION

Habitat loss and fragmentation are globally pervasive processes that have increased in recent decades in the remaining tropical forests of the world (Achard et al. 2002, Fahrig 2003). For example, in Latin America and the Caribbean, Aide et al. (2013) estimated that between 2001 and 2010 deforestation resulted in the conversion of >540 000 km<sup>2</sup> of tropical woody

vegetation into agricultural fields and pastures. Although other large areas also began natural recovery processes during this time (Aide et al. 2013), it may be decades before these areas attain the structure, composition and functionality of the original habitats and ecosystems.

For New World primates, fragmentation poses a major threat to wild populations, given their almost strictly arboreal habits (Rosenberger & Strier 1989).

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Habitat degradation and fragmentation have direct effects on the viability of primate populations via the reduction of potential habitat (Link et al. 2010, Arroyo-Rodríguez et al. 2013, Chapman et al. 2013) and the limitation of gene flow between isolated populations (Templeton et al. 1990, Ganzhorn et al. 2015, Mbora & McPeck 2015). At the same time, habitat degradation and fragmentation also influence the behavior and ecology of primates (see Marsh et al. 2013 and references therein). Amongst Neotropical rainforest vertebrates, spider monkeys (genus *Ateles*) are one of the most threatened taxa (IUCN 2015) and one of the first to go locally extinct in fragmented landscapes (Michalski & Peres 2005). Their long reproductive cycles (females begin reproducing at the age of 7 to 9 yr and have a single offspring every 3 yr) make them vulnerable to drivers of population decline such as habitat loss (Link et al. 2013), hunting (Franzen 2006) and disease (Holzmann et al. 2010). Also, given their large body size (ca. 8 to 10 kg) and reliance on ripe fleshy fruits in their diets, spider monkeys generally require large territories in order to fulfill their energetic needs (Di Fiore et al. 2008). Nonetheless, spider monkeys are able to cope with seasonal variation in fruit availability by adjusting foraging subgroup size (thereby reducing direct competition for feeding resources) and/or by adjusting their diets to include a larger proportion of other complementary and more readily available items, such as young leaves (Di Fiore et al. 2008).

Species with flexible grouping patterns such as spider monkeys and chimpanzees (Symington 1990) can balance the costs and benefits of group living by adjusting their foraging subgroup size to the immediate social and ecological conditions (Lehmann & Boesch 2004, Aureli et al. 2008). Spider monkeys show a high degree of fission–fusion dynamics, in which stable social groups (15 to 55 ind.) frequently break apart into smaller subgroups that vary in size and composition (Symington 1990). Given their frugivorous diet and large body size, fission–fusion association patterns in spider monkeys might allow individuals to reduce intra-group feeding competition by ranging in smaller subgroups during periods of fruit scarcity (Steenbeek et al. 1999, Shimooka 2003, Asensio et al. 2008, 2009). For example, at Tinigua Park, Colombia, spider monkeys ranged, on average, in larger subgroups during the period of fruit abundance than during the period of fruit scarcity, while individuals were more often solitary during low fruit periods (Shimooka 2003).

An alternative and non-exclusive strategy used by spider monkeys for coping with periods of fruit

scarcity is increasing the intake of leaves and other supplementary feeding items during periods of fruit shortage (Castellanos & Chanin 1996, Felton et al. 2008). Spider monkeys are considered ripe fruit 'specialists' because in most studies across their geographical distribution they feed on a wide variety of ripe, fleshy fruits, which generally constitute 75 to 90% of their yearly diet (Di Fiore et al. 2008, González-Zamora et al. 2009). Several studies on spider monkeys have found a positive relationship between habitat-wide fruit availability and fruit consumption (Klein & Klein 1977, Symington 1987, Chapman 1990, Chapman et al. 1995, Stevenson et al. 2000). Nonetheless, spider monkeys that live in areas with contrasting rainfall seasons and marked differences in fruit availability throughout the year can temporarily adjust their diet to rely more heavily on young leaves and other items (Chapman 1987, Symington 1987, Castellanos & Chanin 1996, Stevenson et al. 2000, González-Zamora et al. 2009, Chaves et al. 2011). Finally, spider monkeys complement their frugivorous diet with leaves, flowers, unripe fruit, other plant parts, decayed wood (Klein & Klein 1977, Suarez 2006, Di Fiore et al. 2008), clay from mineral licks (Izawa 1993, Link et al. 2011b) and occasionally, insects (Link 2003).

Habitat fragmentation may have direct and indirect effects on habitat-wide productivity and on the availability of ripe fleshy fruits as smaller fragments are generally associated with modified vegetation structure and composition (Hill & Curran 2003). Small fragments are often lacking in large fruiting trees and have less diverse tree communities, thus reducing their overall fruit productivity and potentially increasing the durations of fruit scarcity periods (Arroyo-Rodríguez & Mandujano 2006). Under these conditions, spider monkeys must rely on more readily available items (e.g. leaves), or on keystone plant species (e.g. *Ficus* spp.) during periods of habitat-wide fruit scarcity (Felton et al. 2008).

To date, most studies on the feeding ecology of spider monkeys have been conducted in forests with little or no human intervention. However, recent studies aiming to compare the diets of spider monkeys in both fragmented and continuous areas have documented that, in a similar way to the dietary response to periods of fruit scarcity, spider monkeys tend to include a larger proportion of leaves in their diet when they are constrained into small forest fragments (González-Zamora et al. 2009). Nonetheless, there is still little information on how they may cope with habitat fragmentation and its long-term implications on the persistence of their wild populations.

Brown spider monkeys *Ateles hybridus* are one of the most endangered primates in the Neotropics (Mittermeier et al. 2009), and only a single previous study has focused on describing their feeding behavior (Link et al. 2012). At Serranía de Las Quinchas, an inter-Andean forest site in northern Colombia, brown spider monkeys fed almost exclusively on ripe, fleshy fruits all year (Link et al. 2012) and only complemented their diet with leaves and other items for approximately 6% of the time they spent feeding. Spider monkeys at Las Quinchas frequently visit mineral licks, in a similar pattern to the behavior of spider monkeys in western Amazonia (Izawa 1993, Link et al. 2011a,b), to obtain complementary nutrients or minerals not readily available in their diets or to mitigate the effects of secondary metabolites contained in leaves and other vegetative parts of plants (Krishnamani & Mahaney 2000).

Here, we describe the diet of 2 groups of brown spider monkeys living in a small forest fragment in the inter-Andean Rio Magdalena valley in northern Colombia. We provide evidence on how Critically Endangered brown spider monkeys are able to cope with the challenges of forest fragmentation and living at high population densities (see Link et al. 2010 for details), and we assess the importance of the availability of fleshy fruits on their dietary composition. This study builds on the existing broad literature on the diets of spider monkeys by documenting the diet of a population of brown spider monkeys living in a heavily fragmented area where the monkeys have also been the subject of long-term, longitudinal study.

## MATERIALS AND METHODS

### Study area

The study site consisted of a small fragment of approximately 65 ha of seasonally flooded, lowland forest (90 m a.s.l.) along the San Juan River, within the floodplains of the Magdalena River in the province of Santander, Colombia (6°42'58.2"N, 74°08'02.7"W). The site was located within Hacienda San Juan del Carare (hereafter San Juan), a private cattle ranch made up of a mosaic of pastures, wetlands and small patches of forest, with an average annual rainfall of 3458 mm. This area has an annual bimodal rainfall cycle, with rainy seasons between March and May and between September and November, and drier seasons between December and February and between June and August. During peak rainy periods, the entire study site floods for periods that range

between a few days to several weeks. The study fragment is covered by ~9 km of mapped and georeferenced trails, and contains over 2000 marked and mapped trees in which spider monkeys were recorded feeding throughout the study.

### Study subjects and field methods

This study was conducted on 2 neighboring groups of brown spider monkeys living in the study fragment. Most of the data was collected on a single study group, SJ-1, which over the course of the study contained 2 to 4 adult males and 5 to 6 adult females and their dependent offspring. The second study group comprised a single adult male and 5 adult females and their dependent offspring at the time of the study.

We conducted dawn-to-dusk behavioral follows and collected systematic data on the feeding behavior of animals from the 2 study groups for approximately 3 yr, from July 2009 through March 2012. Data collection was not continuous throughout the study period, given the intense rainy seasons of 2010 and 2011 which prevented us from collecting data during certain months when flooding made portions of the study fragment inaccessible. We used focal animal sampling (Altmann 1974), attempting to follow a single focal animal for the entire day and balancing focal animal follows in order to have similar sampling for all adults and subadults in the 2 groups.

During behavioral follows, we collected instantaneous point samples of the behavior of our focal subject at 5-min intervals, based on a comprehensive behavioral protocol and ethogram developed during our long-term research on spider monkeys in Colombia and Ecuador (A. Di Fiore & A. Link unpubl. data). Data on the activity patterns of spider monkeys were extracted from these 5-min point samples, in which we recorded 1 out of 5 general activities for the focal individual: (1) feeding, (2) moving, (3) resting, (4) social activities and (5) other non-social activities.

In order to quantify the diet of brown spider monkeys at San Juan, we documented continuous records of all feeding events from our focal animal by recording the start and end time of each feeding bout (thus, its duration), the species or morphospecies consumed, and the item eaten (e.g. fruits, young leaves, etc.). In addition, for all major feeding sources (i.e. those used by the focal animal for >5 min) we tagged the tree with a unique ID number, and we recorded its diameter at breast height (DBH) and spatial location. Locations were recorded by measuring the distance and angle of the tree from one of the

roughly 2500 reference points within the study fragment that had been previously mapped and georeferenced using a handheld GPS with a high sensitivity antenna. We collected botanical vouchers for all trees and lianas included in the diet of brown spider monkeys, and identified them either at the Herbarium at Universidad de Los Andes Natural History Museum or at the Dendrology Laboratory at Universidad del Tolima.

### Forest productivity

We estimated habitat-wide fruit availability within the study fragment by conducting regular phenological surveys and estimating the productivity of ripe fleshy fruits (the main feeding item in spider monkey diets; Di Fiore et al. 2008), following the methods developed by Stevenson (2002). Every 2 wk, we sampled 8 transects covering roughly 6500 linear meters and recorded phenological information for all trees and lianas whose crowns fell within 1 m of the transect line and that were bearing ripe fruits during the particular monitoring cycle. Transects were walked slowly, and fruiting trees and lianas were detected directly by examining the overlying crown or by indirect cues of fruits and flowers in the forest floor. For each fruiting tree, we recorded its DBH, perpendicular distance to the transect, and spatial location along the transect. Each tree was also tagged with a unique ID number. In order to estimate the effective sampling area covered in our surveys, we averaged the perpendicular distance of all fruiting trees from the transect and used this average distance as half the transect width (as it is considered at both sides of the transect), which, multiplied by the total distance covered for each phenological sampling, gave us the total estimated sampling area (see Stevenson 2002 for details).

This research project was conducted under the institutional guidelines from Universidad de Los Andes and the approval of Ministerio de Medio Ambiente y Desarrollo Sostenible, and complied with the ethical standards for the study of endangered primates in their natural habitats.

### Data analyses

We quantified the time spent feeding by spider monkeys throughout the study as the proportion of 5-min point samples in which we recorded the focal animal feeding, divided by the total number of point

samples in the study. Then, based on the continuous feeding records from our focal animal samples, we calculated the proportion of time brown spider monkeys spent feeding on the different food items and on the different species of trees and lianas throughout the study. We partitioned these data by months in order to evaluate variability in the monkeys' feeding strategies across the study period, and to evaluate the effect of fruit availability on their diet. We compared the diets of the 2 study groups, and that of males versus females, using Mann-Whitney *U*-tests.

We employed the 'preference index' proposed by Krebs (1989) and used by Felton et al. (2008) in order to evaluate which trees and lianas were preferred by brown spider monkeys. The index is calculated as:

$$E_i = (r_i - n_i) / (r_i + n_i) \quad (1)$$

where  $r_i$  is the percentage of species  $i$  in the diet, and  $n_i$  is the relative abundance of species  $i$  in the area, which we calculated as the basal area of species  $i$  per ha (Krebs 1989). Preference index values can range between  $-1$  (for avoided trees or lianas) and  $+1$  (for highly preferred trees or lianas). Data on forest structure and diversity were taken from botanical work done at San Juan (Villanueva 2008).

In order to estimate biweekly habitat-wide productivity, we used 2 variables as proxies of fruit availability within the study fragment: (1) the number of fruiting trees and lianas in phenological transects during each period, and (2) the basal area of all fruiting trees and lianas in the transect. Given that the fruiting periods of most tropical trees and lianas may fall in 2 or more biweekly periods, we divided the contribution of each fruiting tree along its fruiting period by assigning a coefficient derived from Pascal triangles (see Stevenson 2002) to each fruiting period and then multiplying this coefficient by its basal area. Thus, a tree fruiting for 3 consecutive periods would have its basal area (as an index of its productivity) assigned 0.25, 0.50 and 0.25 to each of the 3 fruiting periods, respectively. Finally, we used a Spearman's correlation test in order to evaluate the relationship between fruit availability and the proportion of fruits in the diet of brown spider monkeys.

## RESULTS

Overall, we completed 2052 h of focal animal sampling on our 2 study groups (SJ-1: 1890 h; SJ-2: 162 h). Spider monkeys spent most of their time resting (mean  $\pm$  SD: 45.2  $\pm$  6.2%,  $n = 20$  ind.), and invested almost a quarter of their time feeding (25.9  $\pm$

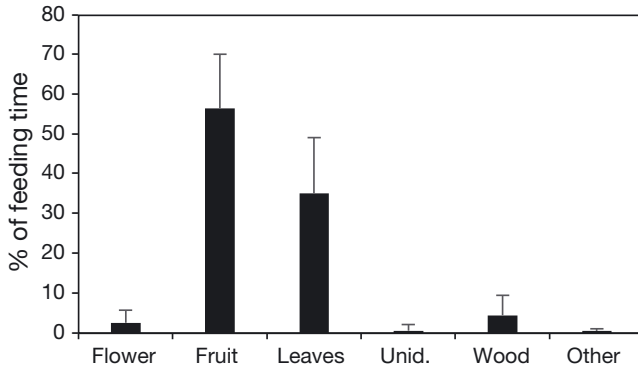


Fig. 1. Diet of brown spider monkeys *Ateles hybridus* in a fragmented forest in San Juan de Carare, Colombia. Bars represent the percentage of feeding time for different items. Error bars show SD. Unid: unidentified

2.8%) and moving (23.8 ± 3.5%), while devoting only a small proportion of their time to social behavior (4.4 ± 4.0%) and other non-social activities (0.6 ± 0.6%). We recorded 4818 feeding bouts in which brown spider monkeys invested a total of 29 651 min (494.2 h) feeding, which accounted for 24% of the total sampling time. The average proportion of time spent feeding by the 14 adult individuals in our main study group was 24.8 ± 3.7% (range: 17.9 to 30.7%) based on the 5-min point samples.

At San Juan de Carare, the diet of brown spider monkeys included items such as ripe fruits, young leaves, flowers, decayed wood, soil from termite

nests and water, amongst others. Although ripe fruits were the most intensively used item, the monkeys spent only 54.1% of their feeding time eating ripe fruits. Consumption of young leaves accounted for 37.2% of their feeding time, while eating flowers from a few species (n = 8) and decayed wood comprised 3.9 and 3.2% of their feeding time, respectively. Only 1.6% of their feeding time was spent on items that were not identified (Fig. 1).

### Temporal variation in diet of brown spider monkeys

Even though behavioral follows had to be interrupted during several months due to floods in the study area, we were able to record the diet of brown spider monkeys at San Juan for a total of 26 mo over a period of 3 yr. Although the temporal variation in the diet of brown spider monkeys at San Juan was not as marked as that of other populations of wild spider monkeys (Chapman et al. 1995, Di Fiore et al. 2008), the consumption of fruits reached monthly levels comparable to that of other *Ateles* populations (up to 74% of the monthly diet). Nonetheless, the proportion of fruits consumed in some months was sometimes quite low, accounting for as little as 34% of their feeding time (Fig. 2). Brown spider monkeys at San Juan ate decayed wood from dead-standing trees during almost all months of the study. Decayed

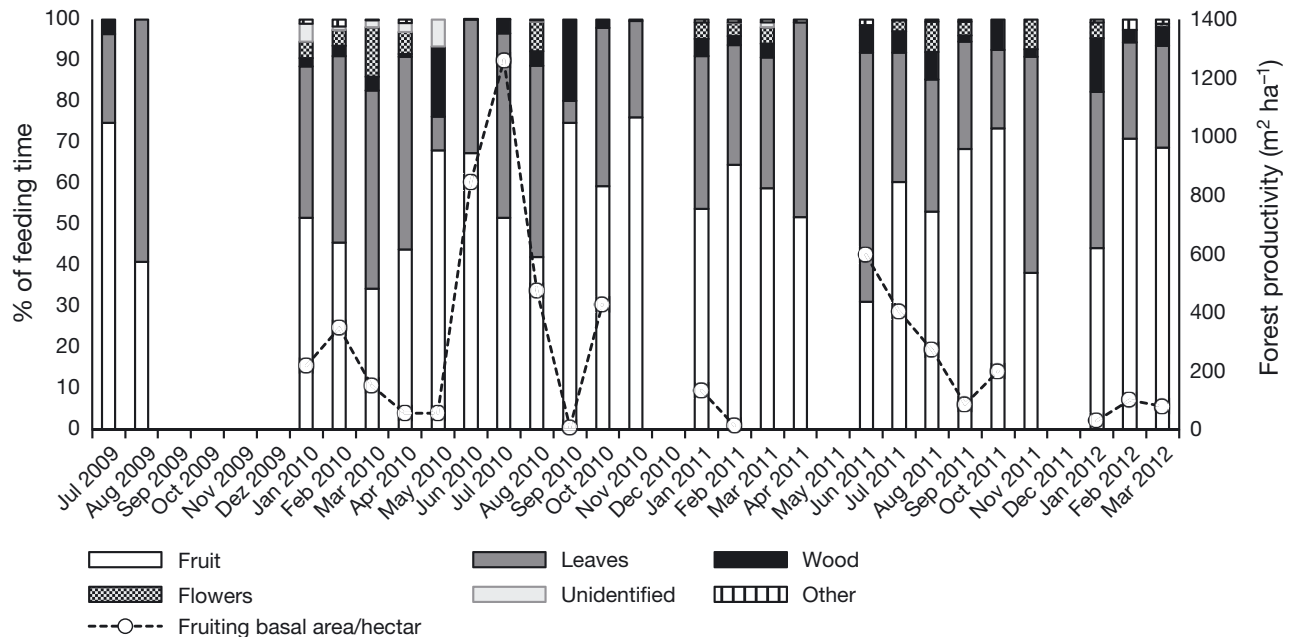


Fig. 2. Monthly proportions of items included in the diet of brown spider monkeys *Ateles hybridus* (bars) and estimates of habitat-wide fruit availability (dashed line) at San Juan de Carare, Colombia

wood represented 3.1% of their overall diet, although in some months it accounted for as much as 12% of their feeding time (Fig. 2). Flowers were also part of brown spider monkeys' diet in 23 of the 26 mo sampled.

### Group, sex and individual variation in diet

Although sampling effort was not evenly divided between study groups, we did not find any differences in the time individuals from each study group spent feeding on different items (flowers: Mann-Whitney  $U = 183$ ,  $p = 0.67$ ; fruits: Mann-Whitney  $U = 3104$ ,  $p = 0.35$ ; leaves: Mann-Whitney  $U = 3121$ ,  $p = 0.46$ ; wood: Mann-Whitney  $U = 236$ ,  $p = 0.92$ ). Also, we did not find differences between the sexes in the proportion of time spent feeding on any particular item (flowers: Mann-Whitney  $U = 414$ ,  $p = 0.19$ ; fruits: Mann-Whitney  $U = 9494$ ,  $p = 0.58$ ; leaves: Mann-Whitney  $U = 9573$ ,  $p = 0.44$ ; wood: Mann-Whitney  $U = 610$ ,  $p = 0.58$ ). In both study groups, ripe fruits were the most common item included in the diet (54% for group SJ-1; 59% for group SJ-2). Leaves also composed a major feeding item in both study groups, accounting for 38 and 32% of the feeding time of SJ-1 and SJ-2, respectively.

### Dietary diversity

The diet of brown spider monkeys at San Juan included at least 55 plant species from 47 different genera and 24 plant families (Table 1). We were unable to identify the plant species consumed for a large percentage of feeding events, corresponding to 23% of feeding time; these were mainly from short feeding bouts (<1 min) where the animals fed on young leaves from canopy lianas. The most important family in the diet was Moraceae, comprising 34.4% of the monkeys' total feeding time and including at least 3 of the most important species in their diet (see below). Other key families in the diet of brown spider monkeys at San Juan included Malvaceae (11.7%), Fabaceae (4.7%), Polygonaceae (4.1%), and Annonaceae (4.1%). Of the 27 plant families included in the diet, only 12 individually accounted for >1% of the total feeding time (Table 1).

In a similar pattern to that described in other studies on spider monkeys, only a handful of species individually constituted a large proportion of their diet. The 5 most intensively consumed species accounted for almost half of the diet (46%). Three figs

(*Ficus dendrocida*, *F. insipida*, and *Ficus* sp. [not identified to species level]) were amongst the most consumed species, contributing to 11.9, 11.8 and 7.5% of the total feeding time, respectively. Other important species included *Guazuma ulmifolia* (10.2% of feeding time) and *Coccoloba lehmannii* (4.1%) (Fig. 3).

Brown spider monkeys fed on fig trees during all 26 mo of the study, and consumption of various parts of fig trees accounted for 31.8% of their time spent feeding. During 17 mo, figs accounted for at least 25% of the monthly diet (Fig. 4), and in 4 mo, figs comprised more than half of their feeding time. Interestingly, the monkeys fed not only on ripe and unripe *Ficus* fruits, but also included a high percentage of leaves during their time feeding on fig trees.

### Habitat-wide fruit availability

During the study period, we recorded a total of 2913 individual trees and lianas from 60 different species that produced ripe fleshy fruits. Given that the average distance of all fruiting trees to the center of the phenological transect was 4.4 m, we estimated our sampling area as 28380 m<sup>2</sup> (2.84 ha). The average fruiting tree density per monitoring period was 30.9 trees ha<sup>-1</sup>, and the average total basal area of trees bearing fruits in each monitoring period was 8576330 cm<sup>2</sup> (Table 2). Across 36 monitoring periods, these 2 variables, used to estimate habitat-wide productivity, were highly correlated (Spearman's  $r = 0.499$ ,  $p = 0.002$ ).

Finally, we did not find a significant relationship between ripe fruit availability and the proportion of ripe fruits included in the brown spider monkeys' diet. When we used the number of fruiting trees per monitoring period as a proxy of fruit availability, we found that there was no relationship between productivity and fruit consumption ( $r = 0.071$ ,  $p = 0.77$ ,  $n = 20$ ) (Fig. 2). When we used the basal area of fruiting trees as a proxy of habitat-wide fruit availability, contrary to our expectations, we found a negative but non-significant relationship between fruit availability and the proportion of the diet made up of ripe fruits (Spearman's  $r = -0.403$ ,  $p = 0.08$ ,  $n = 20$ ) (Fig. 2).

## DISCUSSION

Brown spider monkeys living in the seasonally flooded forest of San Juan have one of the most folivorous and least diverse diets reported for *Ateles*.

Table 1. Species consumed by brown spider monkeys *Ateles hybridus* in the studied forest fragment in San Juan de Carare, For a description of the preference index see 'Materials and methods: Data analyses'. Columbia. FR: fruits; FL: flowers; L: leaves; DW: decayed wood; OT: other

Family	Species	Item	Feeding time (min)	Preference index
Anacardiaceae	<i>Spondias mombin</i> L.	FR	745	-0.58
Annonaceae	<i>Duguetia colombiana</i> Maas	FR, L	123	-0.12
Annonaceae	<i>Oxandra</i> sp.	FR	9	-0.72
Annonaceae	<i>Pseudomalmea boyacana</i> (J.F.Macbr.) Chatrou	FL, FR, L	695	0.71
Annonaceae	<i>Xylopia amazonica</i> R.E. Fr.	FR	371	0.61
Araceae	<i>Anthurium</i> sp.	L	20	
Araceae	<i>Syngonium</i> sp.	L	107	
Arecaceae	<i>Bactris pilosa</i> H. Karst.	FR	18	
Bixaceae	<i>Cochlospermum orinocense</i> (Kunth) Steud.	L	90	
Boraginaceae	<i>Cordia collococca</i> L.	FR	632	0.16
Chrysobalanaceae	<i>Hirtella bicornis</i> Mart. & Zucc.	FR	44	
Chrysobalanaceae	<i>Licania platypus</i> (Hemsl.) Fritsch	FR	68	-0.87
Clusiaceae	<i>Garcinia madruno</i> (Kunth) Hammel	FR	7	
Clusiaceae	<i>Garcinia</i> sp.	FR	9	
Convolvulaceae	<i>Maripa panamensis</i> Hemsl.	FL, FR, L	218	
Fabaceae	<i>Cassia grandis</i> L. f.	FL, FR, L	701	0.45
Fabaceae	<i>Erythrina glauca</i> Willd.	FL, L	44	
Fabaceae	<i>Inga pezizifera</i> Benth.	FR, L	297	0.90
Fabaceae	<i>Inga punctata</i> Willd.	FR, L	3	-0.79
Fabaceae	<i>Machaerium capote</i> Triana ex Dugand	FR, L	165	
Fabaceae	<i>Ormosia colombiana</i> Rudd	L	4	-0.95
Fabaceae	<i>Senegalia polyphylla</i> (DC.) Britton & Rose	L	41	-0.73
Fabaceae	<i>Zygia longifolia</i> (Humb. & Bonpl. ex Willd.) Britton & Rose	L	27	-0.93
Gnetaceae	<i>Gnetum leyboldii</i> Tul.	FR	498	
Lecythidaceae	<i>Gustavia dubia</i> (Kunth) O. Berg	FR	66	0.06
Loganiaceae	<i>Strychnos panamensis</i> Seem.	FR	60	
Loganiaceae	<i>Strychnos</i> sp.	FR	62	
Malvaceae	<i>Guazuma ulmifolia</i> Lam.	FR, L	3007	0.69
Malvaceae	<i>Luehea seemannii</i> Triana & Planch.	L	8	
Malvaceae	<i>Pseudobombax septenatum</i> (Jacq.) Dugand	L	67	0.85
Malvaceae	<i>Vasivaea podocarpa</i> Kuhlman.	FR, L	374	0.80
Meliaceae	<i>Trichilia pallida</i> Sw.	FR	340	0.63
Menispermaceae	<i>Chondodendron tomentosum</i> Ruiz & Pav.	FR	14	
Moraceae	<i>Clarisia biflora</i> Ruiz & Pav.	FL, FR, L	619	0.59
Moraceae	<i>Ficus amazonica</i> (Miq.) Miq.	FR, L	109	
Moraceae	<i>Ficus crassiuscula</i> Warb. ex Standl.	FR, L	39	
Moraceae	<i>Ficus dendrocyda</i> Kunth	FR, L, DW	3504	
Moraceae	<i>Ficus hoja lanceolata</i>	L	28	
Moraceae	<i>Ficus insipida</i> Willd.	FL, FR, L, DW, OT	3482	-0.06
Moraceae	<i>Ficus</i> sp.	FL, FR, L, DW, OT	2210	
Moraceae	<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	FR, L	125	
Moraceae	<i>Sorocea pubivena</i> Hemsl.	FL	38	
Myrtaceae	<i>Eugenia biflora</i> (L.) DC.	FR, L	718	0.95
Polygonaceae	<i>Coccoloba lehmannii</i> Lindau	FR, L	1217	0.81
Rubiaceae	<i>Faramea capillipes</i> Müll. Arg.	FR	4	-0.92
Rubiaceae	<i>Genipa americana</i> L.	FR	176	-0.42
Salicaceae	<i>Laetia corymbulosa</i> Spruce ex Benth.	FR	9	0.11
Salicaceae	<i>Tetrathylacium johanseni</i> Standl.	FR	197	0.64
Sapindaceae	<i>Dilodendron costaricense</i> (Radlk.) A.H. Gentry & Steyerm.	FR	108	-0.02
Sapindaceae	<i>Paullinia bracteosa</i> Radlk.	FR	1	
Sapindaceae	<i>Talisia cerasina</i> (Benth.) Radlk.	FR	14	
Sapotaceae	<i>Chrysophyllum</i> sp.	FR	169	
Sapotaceae	<i>Pouteria baehniiana</i> Monach.	FR	542	0.56
Sapotaceae	<i>Sarcaulus brasiliensis</i> (A. DC.) Eyma	FR	40	
Urticaceae	<i>Cecropia membranacea</i> Trécul	FR, L	230	0.88
Other			195	
Unidentified			6943	

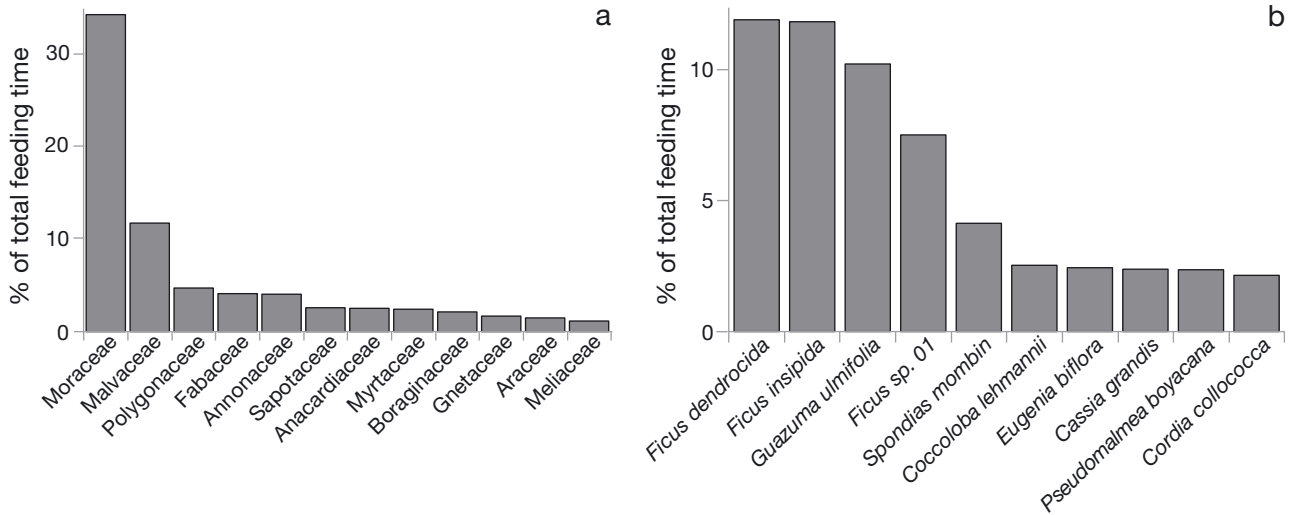


Fig. 3. Most common (a) families and (b) species in the diet of brown spider monkeys *Ateles hybridus* at San Juan de Carare, Colombia

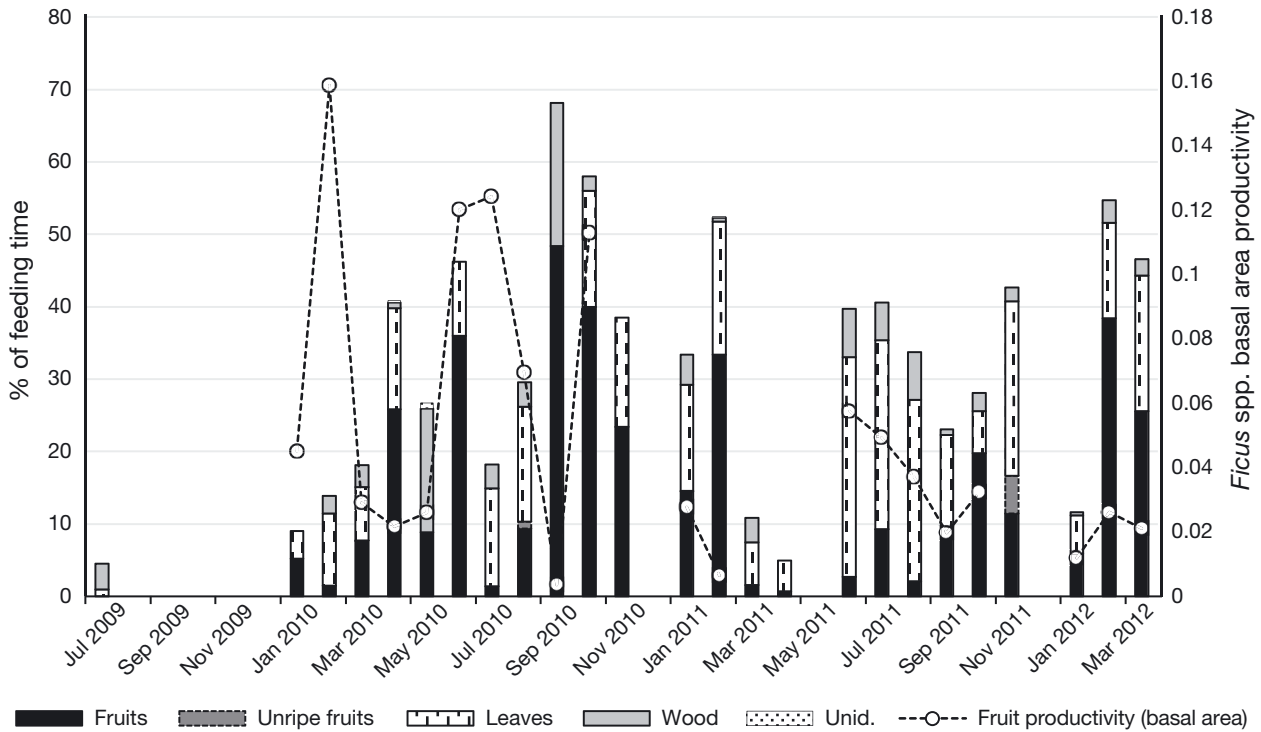


Fig. 4. Feeding time invested by brown spider monkeys *Ateles hybridus* in eating different parts of *Ficus* spp. trees, and *Ficus* spp. productivity. Unid.: unidentified

Contrary to an earlier study on the diet of *A. hybridus* in another inter-Andean forest at Serranía de Las Quinchas approximately 75 km away (Link et al. 2012), brown spider monkeys at San Juan relied heavily on young leaves year-round, and in fact, leaves comprised approximately 37% of their annual diet, with as much as 74% of the animals' time spent

feeding on leaves in some months. Also, contrary to results found by Chaves et al. (2012) on the dietary differences between Central American spider monkeys in which spider monkeys living in smaller fragments tended to diversify their overall diet, the diet of brown spider monkeys at San Juan was less diverse than that of populations living in the less disturbed



Table 2. Monthly forest productivity. Period I: Days 1 to 15 of each month; Period II: Days 16 to the end of the month. Distance: length of the phenological transect each month. Given that some parts of the forest flood, distances can vary across months

Date	Period	Distance (m)	No. of trees	Sampled area (ha)	Density (trees ha <sup>-1</sup> )	Basal area (cm <sup>2</sup> )
Dec-09	I	6457	85	2.84	29.92	451 184.32
Jan-10	I	6307	91	2.77	32.79	249 290.63
	II	6457	47	2.84	16.54	190 145.32
Feb-10	I	6307	48	2.77	17.29	1 532 602.58
	II	3500	7	1.54	4.54	13 710.52
Mar-10	I	6117	73	2.69	27.12	183 667.60
	II	5642	62	2.48	24.97	98 982.08
Apr-10	I	6277	54	2.76	19.55	145 694.80
	II	6267	63	2.75	22.84	64 935.50
May-10	I	6307	36	2.77	12.97	125 892.64
Jun-10	I	6457	104	2.84	36.60	584 775.81
Jul-10	I	6457	157	2.84	55.26	605 245.32
Aug-10	I	6457	230	2.84	80.95	449 262.43
	II	6457	92	2.84	32.38	227 280.49
Sep-10	I	3350	68	1.47	46.13	17 313.35
Oct-10	I	6457	82	2.84	28.86	549 065.85
	II	6307	80	2.77	28.82	550 997.80
Jan-11	I	6307	76	2.77	27.38	112 190.28
	II	6457	72	2.84	25.34	157 732.15
Feb-11	I	4645	19	2.04	9.29	30 566.37
	II	4455	22	1.96	11.22	32 362.18
Jun-11	I	5445	131	2.39	54.67	280 024.09
Jul-11	I	6457	103	2.84	36.25	174 523.67
	II	6457	131	2.84	46.10	305 571.58
Aug-11	I	5445	90	2.39	37.56	161 785.92
	II	6457	105	2.84	36.95	198 366.13
Sep-11	I	5445	43	2.39	17.94	73 715.81
	II	6457	105	2.84	36.95	118 591.39
Oct-11	I	6457	132	2.84	46.46	206 450.75
	II	5445	105	2.39	43.82	108 182.5
Jan-12	I	6117	52	2.69	19.32	44 290.71
	II	4300	27	1.89	14.27	72 030.13
Feb-12	I	4790	40	2.10	18.97	68 260.35
	II	5162	107	2.27	47.10	185 938.86
Mar-12	I	6457	113	2.84	39.77	114 005.86
	II	5467	61	2.40	25.35	91 694.42

forests of Las Quinchas (55 vs. 123 spp.). The lower diversity in the diet of spider monkeys at San Juan may be due to the fact that they inhabit a seasonally flooded forest with lower overall species richness (72.5 species ha<sup>-1</sup>, n = 2) than terra firme forests (160.5 species ha<sup>-1</sup>, n = 4) at las Quinchas (Stevenson et al. 2011). Overall, the diet of spider monkeys at San Juan was less diverse than that found in most other long-term studies of wild spider monkeys (Table 3).

The dietary diversity of brown spider monkeys at San Juan might have been underestimated due to the fact that a large proportion of feeding bouts took place on lianas and epiphytes that we were unable to

identify. For spider monkeys, a folivorous diet might increase the amount and diversity of toxins and secondary metabolites consumed, which could have both direct and indirect influences on their nutrition and health. It may be significant, then, that in most long-term studies spider monkeys are reported to feed on clay from mineral licks (Izawa 1993, Link et al. 2011a,b), which is suggested to be one means by which they cope with the effects of secondary metabolites. Spider monkeys at San Juan and elsewhere are also reported to feed on decayed wood from dead standing trees (Suarez 2006, Di Fiore et al. 2008, Chaves et al. 2012), which may allow them access to additional minerals not otherwise available in their diet (Krishnamani & Mahaney 2000, Ferrari et al. 2008).

In a similar pattern to that reported in most studies on *Ateles*, figs were an extremely important item in the diet of brown spider monkeys. *Ficus* constituted the single most important genus of plant consumed by brown spider monkeys, averaging 24.1% of their diet across months and reaching up to 68.1% of the monthly time devoted to feeding (Fig. 4). At La Chonta in lowland Bolivia, spider monkeys also relied heavily on figs in their diet, leading Felton et al. (2008) to propose that figs were staple food items, as they were available almost all year, and monkeys fed on them even during periods of fruit abundance. Based on the results of our study, figs at San Juan can also be considered staple food items, as they were present in the diet of brown spider monkeys throughout the study. At San Juan, spider monkeys fed on both ripe and unripe fruits

(also see Felton et al. 2008), and they also heavily relied on young leaves from *Ficus dendroica* and *F. insipida* year-round.

Although at other sites spider monkeys have been reported to include a large proportion of leaves during periods of fruit scarcity (Symington 1987, Chapman & Chapman 1990, Wallace 2005) and when living in disturbed and fragmented habitats (González-Zamora et al. 2009, Chaves et al. 2012), there is scant information on the potential effects of extensive leaf consumption on their reproduction and health. This is particularly relevant given the fact that at San Juan, spider monkeys do not invest large portions of their time in resting and processing the large quan-

Table 3. Dietary composition data of *Ateles* spp. Sources: 1: Cant (1977); 2: Chapman et al. (1995); 3: Campbell (2000); 4: van Roosmalen (1985); 5: Nunes (1998); 6: Russo et al. (2005); 7: A. Link (unpubl. data); 8: Klein & Klein (1977); 9: Suarez (2006); 10: A. Link & A. Di Fiore (unpubl. data); 11: Castellanos & Chanin (1996); 12: Symington (1987); 13: Wallace (2005); 14: Felton et al. (2008); 15: Link et al. (2012); 16: present study

Species/Location	Country	Study length (mo)	No. of species	% Fruits		% Leaves		% Flowers		% Prey		% Other		Source
				Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
<b><i>A. belzebuch belzebuch</i></b>														
Ilha de Maraca, Roraima	Brasil	12	62	88.5	74–98	8.3	0–26	–	–	0	0	3.2	–	5
Tinigua National Park	Colombia	12	106	74	–	12	–	5	–	0	–	9	–	6
Tinigua National Park	Colombia	13	117	73.0	41–96	13.0	3–25	12.0	1–36	1.4	0–9	1.2	0–4	7
La Macarena National Park	Colombia	10	–	83	78–100	7	0–22	<1	–	0	–	10	0–18	8
Yasuni National Park	Ecuador	17	238	78.8	52–92	7.7	0–22	3.2	0–24	0	0	10.3	0–24	9
Yasuni National Park	Ecuador	11	>200	79.4	60–100	12.4	0–23	2.7	0–10	0	0	5.5	0–20	10
Reserva El Caura	Venezuela	12	83	–	–	–	–	–	–	–	–	–	–	11
<b><i>A. belzebuch chamek</i></b>														
Manu National Park	Peru	12	125	74.7	54–99	15.5	<1–38	4.5	0–22	0	0	4.5	0–21	12
Lago Caiman, Noel Kempff	Bolivia	11	75	85.7	63–99	10.7	1–37	2.9	0–16	–	–	0.6	0–3	13
La Chonta	Bolivia	9	63	82.0	–	13.0	–	4.7	–	<1	–	0	0	14
<b><i>A. geoffroyi</i></b>														
Tikal National Park	Guatemala	9	30	54.9	31–84	15.1	1–34	6.3	0–22	1.9	0–17	21.8	1–66	1
Santa Rosa National Park	Costa Rica	38	–	71.4	14–100	12.5	0–86	14.0	–	2.1	0–30	0	0	2
Barro Colorado Island	Panama	14	107	82.2	69–91	17.2	6–32	1.0	0–9	0.6	0–2	0	0	3
<b><i>A. hybridus</i></b>														
El Paujil Private Reserve	Colombia	12	123	91.7	77–100	7.4	–	0	0	0	0	0.7	–	15
San Juan de Carare	Colombia	26	55	54.1	14–76	37.2	5–60	3.9	0–12	0	0	4.8	0–20	16
<b><i>A. paniscus</i></b>														
Voltzberg Nature Reserve	Surinam	26	207	79.8	54–92	7.9	1–23	6.4	1–28	<1	–	5.6	1–17	4

tivity of leaves in their diet. The digestive system of spider monkeys seems best suited for feeding on fleshy ripe fruits—they have very short gut passage times (ca. 4.5 h; Link & Di Fiore 2006) and they also generally feed on leaves prior to long resting bouts, where their metabolism is lower and there may be more time for leaves to be efficiently processed in their digestive system (Chapman 1995). Thus, spider monkeys may be physiologically restricted as to the amount of leaves they can include in their diet. In fact, Wallace (2005) found that during periods when spider monkeys relied most heavily on leaves, their body condition seemed to deteriorate. Given that habitat fragmentation is pervasive across the areas within the historical distribution of spider monkeys (see Link et al. 2013), there is an urgent need to better understand the effect of fragmentation and habitat degradation—not only on spider monkeys' feeding ecology, but also on their long-term population dynamics. Under the suboptimal conditions of a low-quality diet in fragmented landscapes, spider monkeys may develop more slowly or experience longer inter-birth intervals. They may also face increased stress levels, higher parasitic loads (Rimbach et al. 2015) and even lower survival in fragmented landscapes, which, coupled with hunting and other anthropogenic factors, may increase the risk of local extinctions.

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