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The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia

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ABSTRACT

Selective harvesting of timber can lead to population declines in some primate species. As frugivorous primates are important seed dispersers in tropical forests, the reduction of their populations may affect the ecological sustainability of selectively logged forests. This paper is the first to quantify the importance of timber tree species in the diet and nutritional ecology of a primate species. We studied spider monkeys (*Ateles chamek*) inhabiting a certified forestry concession in Bolivia where post-logging population declines of this species have been recorded. We show that spider monkeys occupying unlogged areas obtained approximately 50% of their total intake of macro-nutrients from timber tree species and exhibited a distinct preference for foraging within trees that were of harvestable size. Timber tree species dominated the spider monkeys' diet both during peak fruiting periods and during periods of fruit scarcity. We estimate that under current timber extraction intensities spider monkeys lose significant proportions of their food sources. Our results indicate that further extraction limits could be considered for *Ficus boliviana*, *Spondias mombin* and *Pouteria nemorosa*. We suggest that to ensure long-term ecological sustainability of certified forestry concessions, the importance of timber tree species in the ecology of seed dispersers needs to be taken into account.

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1. Introduction

Approximately six million hectares of tropical forests are selectively logged every year (Asner et al., 2005; Foley et al., 2007). Associated changes to forest structure and plant species composition can lead to significant declines in populations of forest-dependent primates (e.g. Grieser Johns, 1997; Bawa and Seidler, 1998; Chapman et al., 2000). The extent to which selective logging impacts on primates depends in part on the type and frequency of selective logging procedures conducted, the timber species removed, and the primate species considered.

Reduced-impact logging (RIL) is a modified form of selective logging that incorporates a variety of techniques aimed at lowering levels of damage to the residual stand (Heinrich, 1995; Uhl et al., 1997; Putz et al., 2001). The expectation is that these actions, in combination with strict hunting bans, will greatly reduce logging-related impacts on forest-dependent species, including species

sensitive to conventional logging (Putz et al., 2001). Identifying the cause of those population declines in RIL concessions that do occur can help in the continued improvement of RIL standards.

The primate species which are considered to be most vulnerable to selective logging are arboreal, large-bodied, ripe fruit specialists, with slow reproductive rates, and large home ranges (Johns and Skorupa, 1987; Symington, 1988a; Peres, 1994a; Sorensen and Fedigan, 2000; Felton et al., 2003). For these types of species, associated population declines in selectively logged forests are thought to result from the loss of significant amounts of food resources (Johns, 1986; Marsh et al., 1987; Oates, 1996; Felton et al., 2003), alteration of the nutritional quality of food (Rode et al., 2006), and disruption of canopy pathways (Marsh et al., 1987; Gebo and Chapman, 1995; Felton et al., 2003).

Spider monkeys (genus *Ateles*, subfamily Atelinae) are canopy dwelling frugivores found in Neotropical forests, and they have frequently been identified as sensitive to habitat degradation (Johns and Skorupa, 1987; Symington, 1988a; Plumtre and Grieser Johns, 2001). Spider monkeys are also strongly territorial (Valero et al., 2006) which reduces the possibility for spatial adjustments during and after logging. Surveys conducted in the certified RIL forestry concession La Chonta in Bolivia, showed that forest that had been logged 1 and 2 years previously contained only

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25% of spider monkey population densities found in comparable unlogged sections (Fredericksen et al., 2007). Although long-term data in this case are lacking, rapid and dramatic changes in population densities for any species exhibiting strong territoriality and slow reproductive rates are worthy of concern. When that species is also a large-bodied seed disperser, then declines in their population may have long-term negative impacts on the forest ecosystem itself (Chapman and Chapman, 1996; Chapman and Onderdonk, 1998; Babweteera and Brown, 2009).

In order to address one of the potential causes of spider monkey population decline in forestry concessions, we document the role of timber tree species (TTS) in the diet and nutritional ecology of *A. chamek* in the La Chonta forestry concession. To our knowledge this is the first comprehensive analysis of the nutritional contributions of timber trees to a primate species. We present our results using three food/diet categories (not mutually exclusive):

- (i) *staple foods*: foods which are fed upon all year-round independently of the availability of preferred foods (Knott, 2005; Marshall and Wrangham, 2007)
- (ii) *peak season diet*: foods consumed during the period of peak fruit abundance (Felton et al., 2009b)
- (iii) *fall-back diet*: foods of high abundance consumed when preferred foods are scarce (Marshall and Wrangham, 2007)

We place our findings in the context of actual timber extraction rates from this forest and speculate with regards to the likely impact of RIL on food resources for *Ateles chamek*. We discuss forest management practices which may be disproportionately detrimental to spider monkey populations.

2. Materials and methods

2.1. Study area

The study area (S: 15°36'26"–15°37'45" and W: 62°46'59"–62°47'56") was located in the 100,000 ha concession La Chonta, Departamento Santa Cruz, Bolivia. The concession is owned and managed by Agroindustria Forestal La Chonta Ltda, and certified by Smartwood®. This lowland semi-deciduous tropical moist forest occurs in a transitional zone between dry and wet forest (Peña-Claros et al., 2007). The average annual temperature and precipitation for La Chonta is 25 °C and 1580 mm, with 4 months receiving <100 mm (May–September). The seasonal distribution of rainfall during this study was not aberrant (Felton et al., 2008c).

We detected three distinct phenological periods in this forest during the course of this field study: an initial period of high ripe fruit abundance (late wet season, February to mid-April) followed by a 10-week long period of fruit scarcity (early–mid dry season, mid-April to June) before ripe fruit became more abundant again (late dry–early wet season, July to September).

The concession was selectively logged for mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela odorata*) 10–25 years prior to this study (Fredericksen, 2000; Quevedo, 2006). These two species do not produce fleshy fruits and are not spider monkey food sources. Our study area (ca 1.5 km × 2.5 km, covering the spider monkey territory) was situated at least 2 km from areas commercially logged by the current concession owners, and more than 8 km from the closest active harvesting. Hunting is strictly prohibited and enforced within the concession.

2.2. Study subjects

Spider monkeys (genus *Ateles*, subfamily Atelinae) are found in varying forest types from ever-green rainforest to deciduous forests throughout Central and South America (Kinzey, 1997). They

are diurnal, arboreal, frugivorous, and large-bodied primates (7.5–9 kg) (Kinzey, 1997; Smith and Jungers, 1997). The largest social unit of the spider monkey society is called a community, and normally includes 15–40 individuals (Campbell, 2008). Communities split into subgroups during the day according to a fission–fusion pattern of social structure (Symington, 1988b; Chapman, 1990). Our study community consisted of 48–55 individuals.

2.3. Harvesting procedure

Approximately 2500 ha is annually harvested in La Chonta over three 850 ha blocks (Jackson et al., 2002). Average harvest intensity in this forest is 4 trees/ha, average harvest volumes are 6 m³/ha, and the intended rotation time is 25–30 years (Jackson et al., 2002; Peña-Claros et al., 2007). Approximately 160 tree species have been identified at La Chonta, 23 of which are commercially valuable (Peña-Claros et al., 2007).

One year prior to logging, trees that are selected for felling are cleared of all vines and climbers. The minimum size for harvest (MCD = minimum cut diameter) is 70 cm diameter at breast height (dbh) for *Ficus boliviana* and *Hura crepitans*, and 50 cm dbh for all other species. Approximately 20% of target species above MCD are left as seed trees/future crop trees (Jackson et al., 2002).

The territory of our study community was located within part of a logging block that was inventoried for harvestable trees during 2005 and subsequently logged in 2006. In this paper, we include information regarding the inventory of this block and the extraction of timber from all three blocks logged during 2006.

2.4. Study design

We used a trail network covering the study community's territory (360–400 ha) for conducting follows, monthly phenology surveys and detailed vegetation surveys. Within 71 0.1 ha plots distributed throughout the territory, we recorded basal area of all trees >10 cm dbh. Tree density and basal area information derived indicated the availability of certain food and timber species within the territory (see Felton et al., 2008c).

2.5. Feeding observations

Following 5 months of habituating the study community, we collected feeding data February–September 2004. We conducted continuous observations of focal animals (FAs) from dawn to dusk, alternating between 8 males and 10 females. Females were either lactating or pregnant while caring for a juvenile. We followed 10–15 of the FAs for a whole day each month. We noted exact duration of each feeding event and recorded feeding rates (number of items consumed/min) for all food types (mean number of replicates: 10; range 1–107). We used feeding rates to calculate food intake when we could not count the actual number of food items eaten. We identified and tagged all plants that the monkeys ate.

For the purpose of the nutritional analysis presented in this paper we include 51 days where (i) the FA was successfully followed all day; (ii) all feeding events were documented in detail, and (iii) relevant analyses existed for all foods consumed (32 days of 8 females, 19 days of 8 males). We also use data from an additional 19 partial follow days when presenting the proportional use of various food sources in terms of time and total dry matter intake.

2.6. Food collection and laboratory analyses

We collected food items from marked feed trees and dried samples in a drying oven (40–50 °C). For this analysis, 69

different food types were included, representing 35 plant species (a mean of 2.4 individuals per species were sampled (range 1–9)). A sub-sample of food items were chemically analyzed for total nitrogen, lipid, water-soluble carbohydrates, starch, neutral detergent fiber, ash, PEG-binding (polyethylene glycol) capacity, and in vitro digestible nitrogen and dry matter. We estimated “available protein” as (total N) × (in vitro N digestibility) × 6.25. There is some uncertainty whether 6.25 is the best conversion factor for tropical fruits (Milton and Dintzis, 1981), but we use it here to allow for comparison with other studies. We assumed that lipids were 100% available. Values for water-soluble carbohydrates and starch are combined and presented as total non-structural carbohydrates (TNC). See Felton et al. (2009a) for details.

2.7. Data analysis

Nutrient intake from each feeding event was estimated by multiplying ingestion time with the corresponding feeding rate and the nutrient present per item (Felton et al., 2009a). We summed feeding events to obtain the daily nutrient intake and calculated the nutritional contributions of each plant species per season. We calculated the percentage of the population of each TTS that were used during the study period.

By using tree density information we estimated how many harvestable individual trees (≥MCD), belonging to TTS which constituted major food sources, existed within the spider monkey's territory. We estimated the decrease of this resource from the territory under three different harvesting scenarios based on available data: (A) mean rates from the entire 2006 logging area (data provided by Agroindustria Forestal La Chonta Ltda); (B) mean rates from 1998 logging blocks (data reported in Pariona et al., 2003), and (C) the maximum legal harvesting limit which is 80% of existing harvestable trees (of permitted species, suitable shape and condition) that are equal or above MCD (M. Peña-Claros, pers. comm.).

3. Results

3.1. General contributions of timber tree species to diet

Spider monkeys were observed to consume fruit, leaves and flowers from 63 plant species. Ten of these species were logged in the concession (Table 1). Spider monkeys spent 47% of their feeding time in these TTS. TTS provided individuals with ~50% of their total intake of non-structural carbohydrates (TNC), lipids and available protein (Table 1). Daily intake of food items from TTS ranged between 0 and 100% of total dry mass (mean 131 g DM/day sourced from TTS).

Spider monkeys ingested whole seeds of TTS and defecated them intact. In no instance did we observe mastication of seeds. In some cases, spider monkeys ingested small emerging fruits of *F. boliviana* and *Pseudolmedia laevis* (3.8% and <0.1% of fruit eating time, respectively), whose seeds may have been vulnerable to digestion due to their immaturity.

3.2. Contributions of timber tree species in seasonal diets

F. boliviana played a major role in the diet during 6 of the 8 sample months (Table 1). This species provided spider monkeys with more available protein, lipids, fiber, inorganic material and water than any other plant species. Spider monkeys obtained almost 90% of their non-protein energy (TNC + lipids) from fruits of TTS, primarily sourced from *Spondias mombin* and *Pouteria nemorosa*, during the late wet season when the general availability of ripe fruit was high in the territory (their late peak season diet,

Table 1
The contributions by ten commercial timber tree species to the total nutritional intake by spider monkeys. Full follow days were used in this summary (n=51), unless otherwise specified.

Species	Family	Items consumed ^a	%time	%DM	%water	%ash	%AP	%TNC	%lipids	%NDF	BA/ha	#trees/ha	#m
<i>Ficus boliviana</i> C.C. Berg	Moraceae	EB, I, MR, R, LB, YL, L	28.59	22.78	15.6	34.2	23.2	10.1	25.6	31.6	1.6	1.9	6
<i>Pseudolmedia laevis</i> J.F. Macbride	Moraceae	EB, I, MR, R, FB, YL	9.36	16.41	19.1	11.6	14.4	27.9	8.4	11.3	4.4	109.3	3
<i>Pouteria nemorosa</i> ^b Baehni	Sapotaceae	R	4.08	3.58	6.1	2.8	2.2	6.2	5.2	0.6	0.6	6.1	2
<i>Batocarpus amazonicus</i> (Ducke) Fosb.	Moraceae	R, YL, L	2.28	2.04	1.7	3.0	3.6	0.6	2.9	3.6	0.1	0.9	1
<i>Spondias mombin</i> L.	Anacardiaceae	R	1.94	5.08	5.3	4.4	2.2	8.4	4.9	1.4	0.3	1.5	2
<i>Ampelocera Ruizii</i> ^b Klotzsch	Ulmaceae	R, YL, L, F	0.3	0.28	0.08	0.18	0.72	0.02	0.12	0.14	1.6	19.0	4
<i>Terminalia oblonga</i> (Ruiz and Pavón) St.	Combretaceae	YL, L	0.09	1.17	1.0	2.2	2.8	0.3	2.1	2.1	1.7	17.0	2
<i>Caesalpinia pluviosa</i> DC.	Caesalpinaceae	YL	0.01	0.03	c	d	c	d	d	d	0.3	4.3	1
<i>Pouteria macrophylla</i> ^b (Lam.) Eyma	Sapotaceae	R	d	d	d	d	d	d	d	d	0.9	13.6	d
<i>Cordia alliodora</i> ^b (Ruiz and Pavón) Oken	Boraginaceae	R	d	d	d	d	d	d	d	d	0.3	3.6	d
Timber tree species total	47	51	49	58	49	54	49	51					

Column headings: items consumed: EB = emerging fruit bud; I = immature fruit; MR = medium ripe fruit; R = ripe fruit; FB = flower bud; LB = leaf bud; YL = young leaf; L = mature leaf; %time = percentage of total feeding time incl. partial follow days; %DM = percentage of total dry matter intake, incl. partial follow days; water = proportion of fresh weight; AP = available protein estimated from in vitro assay (available N × 6.25); TNC = total non-structural carbohydrates (water-soluble carbohydrates + starch); NDF = neutral detergent fiber; #trees/ha = density of species as an average across the entire territory of the study community; BA/ha = basal area (m²) per ha; m = number of months the species occurred in the diet of spider monkeys (total = 8 months of detailed data collection).

^a Observations from the entire study period including habituation.
^b The relative importance of species to spider monkey diet may have been underestimated as their fruiting period overlapped only partially or not at all with behavioral data collection, or their crop was damaged during 2004 (*P. nemorosa*).
^c No observations during full follow days.
^d Feeding observations were made during habituation, therefore no detailed information available.

Table 2
Seasonal use of timber tree species (TTS) by spider monkeys in La Chonta. Data from full day follows were used for this summary (n = 51).

Seasonal diet	Items consumed	%time	%DM	%water	%ash	%AP	%TNC	%lipids	%NDF
Late peak season diet (late wet season; 5 FAD; 24/2–6/4)									
<i>Spondias mombin</i>	R	22.6	45.8	36.8	44.1	20.8	47.5	38.3	36.6
<i>Pouteria nemorosa</i> ^a	R (MR+R)	45.1	35.0	46.0	31.0	23.0	37.5	44.0	18.2
<i>Ficus boliviana</i>	I, R	5.2	5.5	3.3	10.4	7.3	1.2	5.8	21.7
% TTS of season total		73	86	86	85	51	86	88	77
Fall-back diet (early-mid dry season; 19 FAD; 10/4–28/6)									
<i>Ficus boliviana</i>	EB, I, R, YL	28.8	25.5	18.6	35.1	24.1	10.3	37.5	36.5
<i>Batocarpus amazonicus</i> ^a	LB+YL	4.0	3.2	2.8	4.2	5.5	1.1	5.4	5.2
<i>Pseudolmedia laevis</i>	FB	7.8	1.1	0.9	1.8	1.3	0.5	1.6	1.5
<i>Spondias mombin</i>	R	0.5	1.1	1.2	0.9	0.5	2.1	1.3	0.3
% TTS of season total		41	31	23	42	31	14	46	44
Early peak season diet (late dry–early wet season; 27 FAD; 12/7–15/9)									
<i>Pseudolmedia laevis</i>	R, FB, MR, EB, I, YL	13.5	30.2	35.8	21.8	26.3	54.3	14.6	18.9
<i>Ficus boliviana</i>	LB, EB, R, MR, I	30.1	22.7	15.7	35.3	24.4	11.3	23.7	27.6
<i>Terminalia oblonga</i>	YL, L	0.2	2.2	1.9	4.3	5.5	0.5	3.9	3.6
<i>Batocarpus amazonicus</i> ^a	LB+YL	2.2	1.7	1.5	2.7	3.1	0.6	2.5	2.9
<i>Ampelocera ruizii</i> ^a	YL	0.3	0.2	0.1	0.3	1.2	0.0	0.2	0.2
% TTS of season total		46	57	55	65	60	67	45	53

Column headings: see explanations in Table 1.

^a The relative importance of species to spider monkey diet may have been underestimated as their fruiting period overlapped only partially or not at all with behavioral data collection (*A. ruizii*, *B. amazonicus*), or their crop was damaged during 2004 (*P. nemorosa*).

Table 2). During the 10-week long period of relative fruit scarcity (the early-mid dry season), TTS were part of the fall-back diet and provided spider monkeys with a third of their available protein, and almost half of their lipids primarily sourced from *F. boliviana* (Table 2). We refer to the diet eaten during the late dry–early wet season, when ripe fruit became more abundant again, as their early peak season diet. Timber tree species contributed with 60% of available protein and 67% of TNC to the early peak season diet. Fruiting of the TTS *Batocarpus amazonicus* and *Ampelocera ruizii* did not occur during data collection, thus their importance to the community's diet is unknown.

3.3. Sizes of food trees and timber trees

Of the 544 tagged food plants used (excluding lianas and palm trees), 58% were TTS. Spider monkeys used *F. boliviana* trees that were 22–300 cm dbh (mean = 131 cm, stdev = 69 cm, n = 56, Fig. 1). The majority of tagged individuals of *F. boliviana* (75%), *P. nemorosa* (91%) and *S. mombin* (77%) were ≥MCD (Fig. 1).

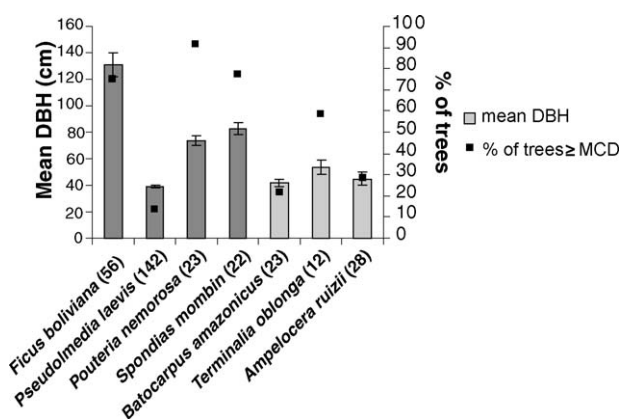


Fig. 1. Mean (±1 SE) diameter at breast height (dbh) of seven timber tree species that were observed to be used by the spider monkeys during the study period. Also indicated is the proportion of trees that were above or equal to the minimum cut diameter (MCD). The number of tree individuals used by the spider monkey community is in brackets. Dark shading = major food species (contributing >2% of total feeding time); light shading = minor food species (<2% of total feeding time).

3.4. Harvesting information from La Chonta

3.4.1. Inventory

Included in the logging company's pre-logging inventory of commercially valuable tree species, were two of the spider monkeys' major food species (species that seasonally contributed with >25% of total dry matter intake) and three minor food species (≤2% of total dry matter intake) (Table 3).

3.4.2. Timber extraction

During the 2006 harvesting season, 2136 trees were extracted from 2445 ha, partly overlapping with our study area. Average harvesting intensity was 0.87 trees/ha and 3.2 m³ wood/ha (not including wood left on forest floor). Twenty percent of harvested stems belonged to species used as food sources (Table 3). Averaged across the whole logging area of 2006, *F. boliviana* was the 5th most commonly extracted tree species (Table 3).

3.5. Estimations of food tree loss

During the study period, we observed the spider monkeys to use between 4 and 8% of the harvestable individuals of the four timber tree species which constituted major food sources (Table 4). The estimated loss of these trees from the spider monkey territory varied greatly depending on the harvesting scenario considered (Table 4).

4. Discussion

Our results showed that timber tree species (TTS) comprised the spider monkeys' staple food, dominated their peak season diet, and also played a significant part in their fall-back diet during the period of fruit scarcity. Spider monkeys spent 47% of their feeding time consuming food items from TTS. These tree species provided approximately half of the spider monkeys' total intake of macronutrients. Furthermore, spider monkeys exhibited a distinct preference for foraging within timber trees that were large enough to be harvested.

The primary staple food resource for this community was figs of the TTS *F. boliviana*. These figs played a major role in their diet for 6 of the 8 months of study, and provided them with more protein,

Table 3
Timber species inventoried and/or extracted from La Chonta during 2006. Species are sorted by harvesting intensity. Also indicated is whether these timber species provided food for spider monkeys during the study period.

Tree species	Family	# trees/100 ha ^a	% of total ^b	Food source
<i>Cariniana ianeirensis</i> Knuth	Lecythidaceae	28.1	32.2	No
<i>Hura crepitans</i> L.	Euphorbiaceae	17.3	19.9	No
<i>Cariniana estrellensis</i> (Raddi) Kuntze	Lecythidaceae	15.7	18.0	No
<i>Terminalia oblonga</i> Steudel	Combretaceae	10.6	12.1	Minor
<i>Ficus boliviana</i> L.	Moraceae	5.6	6.4	Major
<i>Schizolobium amazonicum</i> Huber ex Ducke	Ceasalpinaceae	4.2	4.8	No
<i>Maclura tinctoria</i> (L.) D. Don ex Steudel	Moraceae	1.7	1.9	No
<i>Sterculia</i> sp.	Sterculiaceae	1.6	1.9	No
<i>Hymenaea courbaril</i> L.	Ceasalpinaceae	0.9	1.0	No
<i>Caesalpinia pluviosa</i> DC.	Ceasalpinaceae	0.7	0.8	Minor
<i>Pseudolmedia laevis</i> J. F. Macbride	Moraceae	0.5	0.6	Major
<i>Anadenanthera colubrina</i> (Vell. Conc.) Benth.	Mimosaceae	0.3	0.3	No
<i>Tabebuia lapacho</i> (K. Schum.) Sandwith	Bignoniaceae	0.2	0.2	No
<i>Batocarpus amazonicum</i> (Ducke) Fosb.	Moraceae	0.0	0.0	Minor
Grand total		87.4		
Total food species		17.4	19.9	
Total major food species		6.1	6.9	

^a # trees extracted per 100 ha of the 2006 logging area (total area = 2445 ha).

^b % extracted trees per species of total extracted in 2006.

Table 4
Estimated loss of harvestable trees used by spider monkeys as major food resources (assuming a 400 ha territory), under three different logging scenarios.

Diet category ^a	Staple	Late peak season		Fall-back/early peak season
	<i>Ficus boliviana</i>	<i>Pouteria nemorosa</i>	<i>Spondias mombin</i>	<i>Pseudolmedia laevis</i>
Density of trees >MCD (per ha territory) ^b	1.3	1.0	0.7	1.1
% of existing trees >MCD that were used by SM ^c	8%	5%	6%	4%
(A) # trees extracted/ha in 2006 ^d	0.06	0.00	0.00	0.49
Estimated proportional loss of trees ^e	4%	0%	0%	43%
(B) # trees extracted/ha in 1998 ^f	0.40	0.20	0.20	0.02
Estimated proportional loss of trees ^e	32%	20%	28%	2%
(C) # trees extracted/ha maximum limits ^g	1.01	0.79	0.56	0.90
Estimated proportional loss of trees ^e	80%	80%	80%	80%

^a The tree species presented dominated the diet category given above its name, even though some of the species played part in more than one diet category.

^b Density of tree individuals above minimum cut diameter (MCD) within the spider monkey territory.

^c Proportion of the existing trees >MCD within the territory that were observed to be used by the spider monkeys during the study period.

^d Data from Agroindustria Forestal La Chonta Ltda.

^e Estimated loss of trees (%) from the territory, based on the extraction intensity in question and the percentage of trees >MCD that spider monkeys were observed to use (second data row in table).

^f Data from Pariona et al. (2003).

^g The Bolivian maximum legal limit is to extract 4/5 of all harvestable trees of each timber species.

lipids and inorganic material than any other plant species consumed. Figs from this species were also particularly well balanced nutritionally (Felton et al., 2009a), easily gathered by the monkeys, and readily available both spatially and temporally (Felton et al., 2008c, 2009b). Primate population density can be strongly influenced by the abundance of staple foods (Oates, 1996; Rogers et al., 2004), and fall-back foods (Terborgh, 1983; Marshall and Leighton, 2006). It is possible that the prevalence of *F. boliviana* in the study area contributed to the unusually large size of this spider monkey community.

In addition to comprising the staple food resource, TTS also contributed to the peak season diet and the fall-back diet. At the beginning of the fruiting season their diet was dominated by *P. laevis* and *F. boliviana*. At the end of the fruiting season, *S. mombin* and *P. nemorosa* contributed almost 90% of spider monkeys' TNC and lipid intake. It is notable that so much of the energy intake during the peak fruiting season was provided by TTS. It is likely that spider monkeys, like other ateline primates (Peres, 1994b; Di Fiore and Rodman, 2001), use the peak fruiting season to accumulate fat deposits in preparation for an upcoming period of food scarcity. Such fat reserves may be critical for survival and reproduction in this seasonal environment (Stevenson, 2005). Stored fat was probably used by the spider monkeys during the dry season when

they experienced a 10-week period of relative fruit scarcity. Daily intake of TNC and lipids during this period was 50% of what the spider monkeys consumed during the late fruiting season (Felton et al., 2009b). Four TTS played a substantial role in their fall-back diet and provided a third of their total protein intake.

Because of inter-annual variation in the commercial demand for timber trees, the resulting impact of logging on food resources for a given spider monkey population will vary. In some years, tree harvesting rates would result in the removal of a third of the staple food resource (*F. boliviana*), along with over 20% of the late peak season resource for the population studied (*P. nemorosa* and *S. mombin*). In other years, few individuals of these tree species would be removed, while almost half of *P. laevis* trees used by spider monkeys would be taken from their territory. Logging operations thus substantially reduced the abundance of at least one representative of the three major food/diet categories in any given year. Spider monkey diets are often considered flexible (van Roosmalen, 1985; Chapman, 1987; Symington, 1988b; Cant, 1990; Milton, 1993; Wallace, 2005), and it is possible that they may be able to adjust to the loss of food-providing timber trees by switching to alternative food resources, such as ripe fruit from non-timber species. However, considering that TTS provided this community of spider monkeys with ~50% of their macro-nutrients,

it appears unlikely that non-timber species can adequately compensate this loss at the appropriate times of the year.

Apart from ripe fruit from non-timber species, spider monkeys could potentially switch to a diet containing a greater proportion of vegetative material, predominantly young leaves. Leaves often contain less energy than ripe fruit but could provide valuable protein, especially at times when ripe fruit are rare. However, there are two important factors that are likely to limit the extent to which spider monkeys can switch to leaves, even during the annual lean period. First, their gut morphology limits how much leaf material that can be digested (Milton, 1981). Second, in the Neotropics, young leaves are generally not abundant during the period of ripe fruit scarcity, due to simultaneous peaks in leaf flush and fruit ripening (van Schaik et al., 1993). Because of this synchronicity in fruit and leaf phenology, monkeys have little opportunity to supplement their fall-back diet with a large amount of young leaves. It is also important to note that during the fruit-scarce period the monkeys predominantly sourced alternative food items (leaf buds, flower buds and unripe fruit) from *F. boliviana*. Hence, the most common source of alternative food items was a timber tree species. In conclusion, we suggest that it is unlikely that switching behavior can sufficiently compensate for the loss of dietary food items due to current rates of timber tree removal.

If the switching ability of spider monkeys is indeed limited, we would expect declines in population density after logging has reduced the abundance of important food resources. Fredericksen et al. (2007) reported from the same concession that spider monkey densities were 75% lower in logged forest blocks (logged 1–2 years previously) compared to unlogged blocks. Similarly, population densities of other important seed-dispersing vertebrate taxa, such as howler monkeys, guans (Fredericksen et al., 2007) and toucans (Felton et al., 2008a,b) also exhibited reduced population densities within areas of this forest subjected to reduced-impact logging. Declines of seed dispersers should be of concern to managers of tropical forestry concessions which depend on natural regeneration of commercial timber species (Cowlshaw and Dunbar, 2000; Mason and Putz, 2001).

Spider monkeys are efficient seed dispersers (Dew, 2001) that are known to ingest seeds of several timber species (Wallace, 1998; Felton et al., 2008c). Spider monkeys often deposit seeds far away from the parent plant in a scattered and fertilized spread, and thereby contribute to a relatively high survivorship of excreted seeds (Zhang and Wang, 1995; Forget and Sabatier, 1997; Andresen, 1999; Dew, 2001; Stevenson et al., 2002; Russo et al., 2005). Recent evidence has linked reduced population densities of seed-dispersing monkeys with a significant shift in forest structure (Nunez-Iturri et al., 2008). Furthermore, it does not appear that the seed dispersal services provided by large-bodied monkey species can be readily compensated for by small-bodied monkey species (Peres and Dolman, 2000) or frugivorous birds (Clark et al., 2001). Substantial reductions in the population size of spider monkeys may therefore affect the long-term sustainability of the forestry concession itself. Notably, the Bolivian forestry industry is plagued by inadequate regeneration of the most important timber species, including those tree species addressed in this paper (Mostacedo and Fredericksen, 1999). In the long term, these problems are likely to be exacerbated if the population densities of seed dispersers are further reduced.

Our results lead us to suggest that *F. boliviana*, *S. mombin* and *P. nemorosa* are important resources for spider monkeys and that it is justified to consider placing further limits on their extraction. Although *P. laevis* was also an important food resource, we suggest that this species is of relatively low concern for spider monkey conservation in this forest. This is because it is the most common

tree species, extraction rates are normally low, and spider monkeys rarely use individuals that are large enough to be harvested.

It is important to note that we are addressing only a single harvesting cycle in this analysis. As the current rotation period is 30 years (Peña-Claros et al., 2008) and second harvests are predicted to yield volumes only 28% of the first harvest (Dauber et al., 2005), it is projected that populations of the above mentioned tree species could be further depleted. Furthermore, for the La Chonta forestry concession, the current legal limits for timber extraction are well above the number of stems cut for a given tree species at the time of this study. Therefore, the potential impact of logging operations on these spider monkey communities is based to a large extent on market demand which can change dramatically from one year to the next.

The findings of this study indicate that the loss of important food resources is a causal factor to lower population densities of spider monkeys recorded in logged blocks of the La Chonta concession. We acknowledge that our conclusions are based on nutritional data collected during 1 year from a single community of spider monkeys. This raises the issue as to how far we can generalize from our results both temporally and spatially. With regard to between-year variation in food availability, it is expected that the importance of *F. boliviana*, *S. mombin* and *P. nemorosa* in the spider monkeys diet would vary between years. Further studies would help to clarify the extent of this variation. However, because (1) the level of importance that we report for these timber tree species in the nutritional ecology of this spider monkey community was so high, and (2) the distribution of rainfall during the study was representative of the average monthly rainfall of the forest (Felton et al., 2008c; Agroindustria Forestal La Chonta Ltda, unpubl. data) we suggest that our general conclusions are likely to be robust to inter-annual variations. With regards to the relevance of our findings to other locations, further studies are needed.

Because the maintenance of seed dispersers is critical for ensuring forest regeneration (Chapman and Onderdonk, 1998; Nunez-Iturri et al., 2008), our findings are relevant to the development of sustainable forest management practices, especially in regions where the suite of commercial timber species include those that produce fleshy fruits important to the survival of seed-dispersing animals.

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