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## Does Resource Availability Affect the Diet and Behavior of the Vulnerable Squirrel Monkey, *Saimiri vanzolinii*?

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**Abstract** Seasonal changes in food availability influence the behavior and diet of primates, and an understanding of dietary changes is important for the development of informed conservation plans. *Saimiri vanzolinii* is a small-bodied, omnivorous squirrel monkey endemic to the floodplain forests in Central Amazonia. It has a restricted distribution of only *ca.* 870 km<sup>2</sup> and is classified as Vulnerable. We examined seasonal variation in this species' diet. We collected phenological (presence and absence of ripe fruits from 205 tree species) and dietary and behavioral data for unhabituated groups of *S. vanzolinii* on nine 2-km transects in the floodplain forests of Central Amazonia for 2 years, encompassing the high-water and low-water periods. Fruit availability was higher, and the monkeys traveled less and fed more during the high-water than the low-water period. There were no seasonal differences between the high-water and low-water periods in the time spent feeding on fruits, flowers, or arthropods. *S. vanzolinii* spent more time consuming fruit than arthropods in the high-water period, but this was not the case in the low-water period. These findings suggest that food selection changed between seasons, and *S. vanzolinii* focused more on fruit in the low-water period, when fruit was less available, than in the high-water period, when fruit was more

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available. These results support the predictions of the ecological constraints model.

**Keywords** Feeding behavior · Flooded forest · Phenology · Seasonal changes

## Introduction

One of the most important questions in animal ecology is how the environment, e.g., seasonal changes in food availability, influences the behavior of consumers (Wong and Candolin 2015). Climate and environmental factors determine resource availability, which can affect consumer behavior, reflecting their strategies for using resources (Yang *et al.* 2008). In general, seasonality is much stronger in temperate than in tropical forests (Janzen 1967), but variable food supply drives consumers' responses in both forest types (Hemingway and Bynum 2012). Phenological patterns in tropical forests are influenced by the climate, yielding clear patterns in abundance and scarcity (Mendoza *et al.* 2016). Ecological constraints models propose that primates react to reduced abundance of preferred resources by changing to abundant lower quality fallback resources, increasing their daily journey length to maintain access to scattered preferred resources, or reducing their daily journey length in reaction to the reduced energy intake from lower quality resources (Chapman and Chapman 2000; Marshall and Wrangham 2007; Snaith and Chapman 2007; Marshall *et al.* 2009).

Flooded tropical forests cover 800,000 km<sup>2</sup> (14%) of the Amazon basin (Melack and Hess 2010) and are subject to extreme environmental fluctuations during high-water periods when the bases of trees and often their canopies are submerged by nutrient-rich white waters each year (Furch 1984; Haugaasen and Peres 2005; Junk *et al.* 2012; Klammer 1984; Parolin *et al.* 2011; Schöngart *et al.* 2002). This change in water level is the most important regional seasonal variable (Ayres 1993; Ramalho *et al.* 2009) and involves average annual changes in water level of ca. 10 m, which submerges many trees for more than 230 days every year (Junk 1989). Peak fruit production occurs in the high-water season and the flood pulse also strongly influences the fauna (Hawes and Peres 2014a, b; 2016; Junk 1989).

Studies of the diet of *Saimiri* document seasonal variation in the consumption of different plant parts, i.e., fruit, leaves, and flowers, as well as insect foraging (Araujo 2014; Boinski 1999; Lima and Ferrari 2003; Stone 2007a, b; Terborgh 1983). This variation is strongly influenced by plant resource seasonality (Di Fiore and Campbell 2005; van Schaik *et al.* 1993). Given the extreme difficulties of conducting research in flooded forests, most studies of *Saimiri* ecology have been conducted in unflooded forests (Boinski 1987, 1988, 1999; Lima and Ferrari 2003; Stone 2006, 2007a, b; Terborgh 1983), whereas little information is available on them in flooded forests (Paim and Queiroz 2009; Paim *et al.* 2013).

The floodplain forests along the Solimões River, in Central Amazonia, support 11 primate species (Marsh 2014; Paim *et al.* 2013; Rabelo *et al.*

2014; Valsecchi 2005), including *Saimiri vanzolinii*, which has the smallest distribution range of any Neotropical primate at just ca. 870 km<sup>2</sup> (Paim *et al.* 2013), making it Vulnerable to extinction (Boubli and Rylands 2008; Paim *et al.* 2015). This species is parapatric with *S. cassiquiarensis* and *S. macrodon*, both of which have much larger ranges (Paim *et al.* 2013). We studied the food resources that *S. vanzolinii* use in flooded forests, how the abundance of these resources changes across seasons, and how resource use is affected by flooding. Following patterns documented in other floodplain forests we predicted that 1) ripe fruit availability would be higher during the high-water period, and consequently that *S. vanzolinii* would 2) spend more time eating fruits, 3) spend a larger portion of their feeding time budget consuming fruits than arthropods, and 4) spend less time traveling during the high-water period than during the low-water period.

## Methods

### Study Area

We conducted this study in the Reserva de Desenvolvimento Sustentável Mamirauá (hereafter RDSM; 11,240 km<sup>2</sup>; 03°08′–02°36′S, 65°45′–67°13′W), in one of the most undisturbed areas in Central Amazonia, at the confluence of the Middle Solimões River and the Lower Japurá River (Wittmann *et al.* 2009; Fig. 1), in Brazil. The flood pulse heavily influences the region (Junk *et al.* 1989, 2012) and differentiates four seasons: high-water period (May–July); receding water level (August–September); low-water period (October–January), and rising water level (February–April) (Ramalho *et al.* 2009). We focused on the two extreme water level seasons: low- and high-water periods, taking the water level from the RDSM fluvimetric data base (Instituto de Desenvolvimento Sustentável Mamirauá 2015).

We examined three different habitats in the flooded forest. We derived a classification system that is more easily applied by researchers on foot from a previously described classification that requires a GIS-based landscape analysis (Wittmann *et al.* 2002, 2004): 1) high várzeas: highest areas, subject to annual flooding lasting 2–4 mo, at a water depth of 1.0–2.5 m; 2) low várzeas: areas of intermediate annual flooding that lasts from 4 to 6 mo, at a depth of 2.6 to 5.0 m, and 3) chavascal: extensively flooded areas of shrub vegetation that were inundated 6–8 mo, at a depth of 5.0–7.0 m (Ayres 1993).

### Phenology

We recorded phenological data between the 1st and 7th of each month for 24 consecutive months (October 2012–September 2014) along nine 2-km trails set 1.5 km apart (Fig. 1). The sample constituted 2285 trees with diameter at breast height (DBH)  $\geq 10$  cm, from 205 species, in 72 square plots of 625 m<sup>2</sup> each, set  $\geq 25$  m apart from each other. We monitored 24 plots in each habitat. When possible, we monitored all habitats along the same trail. We only recorded the presence or absence of ripe fruits, as *Saimiri* do not consume unripe fruits. We removed shorter trees from the



**Fig. 1** Map of the geographic distribution of *Saimiri vanzolinii* (dark gray), showing Reserva de Desenvolvimento Sustentável Mamirauá boundaries and the locations of the nine sampling trails.

sample when they were completely submerged during high-water months and effectively not available. The percentage of submerged trees during the high-water period ranged from 3.9% ( $N = 89$  trees in May, 2014) to 13.3% ( $N = 305$  trees in June, 2013).

## Behavior

We sampled the behavior of one group of *Saimiri vanzolinii* on each of the nine phenology trails during each of the 3 mo of each season (high-water period: May–July; low-water period: October–December) for two consecutive years. We did not sample groups more than once in the same month, to avoid temporal pseudoreplication. This gave a total of 54 sampling days in the low-water period and 52 days in the high-water period, with the difference caused by two trails being inaccessible by canoe in July 2014 due to fallen trees. Groups of *S. vanzolinii* were not habituated and we were

unable to distinguish individuals. We could not ascertain whether we observed the same group or a different group on the same trail during different months in the same season. We treated these data as independent in all analyses.

Observations, which started at 07:00 h and ended at 17:00 h, were facilitated by the low level of avoidance behavior exhibited by *Saimiri vanzolinii*. Owing to the unhabituated nature of the groups, the time spent finding a group, and the difficult access to most areas, the time spent continuously observing each group was variable, ranging from 1 to 8 h (mean  $\pm$  SD = 3.1  $\pm$  1.6).

We collected data on foot during the low-water period and by canoe during the high-water period using the same trails. We conducted scan sampling with a scan duration of 3 min and an interval of 10 min when in contact with the group. We recorded behavioral data for all individuals visible during a scan (1–14 individuals per scan, mean  $\pm$  SD = 3.2  $\pm$  1.9) and classified activities as locomotion, feeding, foraging, resting, or social. We acquired 917 scan samples (152 h) in the low-water period and 928 scan samples (153 h) in the high-water period. We collected all consumed plant species for identification in the herbarium at the Instituto Nacional de Pesquisas da Amazônia. We determined species' identities following Boyle *et al.* (2013).

## Data Analysis

We calculated the percentage of fruiting trees for each month by dividing the total number of trees with ripe fruits by the total number of trees sampled in that month, and multiplying by 100. The total number of trees recorded differed between months because some trees died. We analyzed data for all species sampled ( $N = 205$ ), and sampled tree species that were included in the monkeys' diet ( $N = 23$ ). We used a simple linear regression to test the correlation between these two data series, and to confirm the observed pattern indicated for phenology in the flooded forests by other studies (Haugaasen and Peres 2005; Parolin *et al.* 2011; Schöngart *et al.* 2002).

The difficulty of sampling *Saimiri vanzolinii* in flooded forests meant we could not ensure that groups observed on the different trails were independent. To describe the overall diet, we calculated the proportion of all feeding records spent consuming a specific food type (fruits, flowers, and arthropods) per season in each year. To assess differences in activity and feeding budgets between seasons, we calculated the proportion of all data points that fell into one activity category or food type for each trail in a given month and year. We calculated the percentage of time spent feeding on fruits of 23 diet species in each season by dividing the number of fruit records by the number of records for that species in each season, and multiplying by 100.

We used two-tailed *t*-tests to compare the percentage of time spent in each behavioral activity between the high-water period and the low-water period (after arc sine square root transformation). We also used *t*-tests to compare percentage of fruit consumption and arthropods, and percentage of trees fruiting between the seasons. We adjusted the *t*-tests for nonequal variances where appropriate. For both seasons, we used a simple linear regression to test the relationship between proportional use of the 23 sampled species recorded in the diet and 1) the abundance of these same species and 2) the proportion of scans traveling. We performed all statistical tests using SPSS 22.

## Data Availability

All data generated or analyzed during this study are included in this published article (and its Electronic Supplementary Material files).

## Ethical Note

This research complied with protocols approved by the appropriate Institutional Animal Care Committee (Ethical Committee of Instituto de Desenvolvimento Sustentável Mamirauá, under protocol 009/2013). The research adhered to the legal requirements of Brazil, and to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

## Results

The plant species consumed and the proportion of scans in which they were recorded were highly variable (Table I). We observed two fruiting peaks, with the highest peak occurring between February and June and coinciding with the higher water levels, with flooding being longer in 2013 (Fig. 2). We found a strong correlation between fruit abundance in all tree species sampled and the fruit abundance in monkey food species sampled ( $N = 24$ ,  $R = 0.91$ ,  $R^2 = 0.82$ ,  $df = 22$ ,  $P < 0.001$ ). *Saimiri vanzolinii* consumed the fruit of 56 plant species from 26 families, with 34 species used exclusively in the high-water period, 10 species eaten only in the low-water period, and 9 species consumed in both seasons. Of the species consumed, 23 were in our phenology sample. Moraceae was the most important family in their diet during both periods in terms of number of species, and in time spent feeding, with the genus *Ficus* of particular importance (Table I).

The percentage of tree species fruiting for the 23 consumed species was smaller in the low-water period ( $1 \pm SD 1\%$ ) than in the high-water period ( $6 \pm SD 3\%$ ;  $N = 12$ ,  $t = -4.258$ ,  $df = 10$ ,  $P = 0.002$ ). However, the time spent feeding on the fruit of these 23 species did not differ between seasons (low-water period =  $49 \pm SD 14\%$ ; high-water period =  $60 \pm SD 8\%$ ;  $N = 12$ ,  $t = -1.602$ ,  $df = 10$ ,  $P = 0.140$ ; Fig. 3). Use of these 23 species did not correlate with their abundance in the high-water period ( $N = 6$ ,  $R = 0.56$ ,  $R^2 = 0.32$ ,  $df = 4$ ,  $P = 0.238$ ) or low-water period ( $N = 6$ ,  $R = 0.22$ ,  $R^2 = 0.0532$ ,  $df = 4$ ,  $P = 0.669$ ).

We found no seasonal differences in foraging, social activities, or resting behaviors in the full dataset (Table II). *Saimiri vanzolinii* traveled less and fed more in the high-water period, when fruit was more abundant, than in the low-water period (Table II). However, the proportion of scans spent traveling did not correlate with consumed fruit abundance (the 23 species) in the high-water period ( $N = 6$ ,  $R = 0.74$ ,  $R^2 = 0.55$ ,  $df = 4$ ,  $P = 0.087$ ) or low-water period ( $N = 6$ ,  $R = 0.27$ ,  $R^2 = 0.07$ ,  $df = 4$ ,  $P = 0.604$ ).

There were no seasonal differences between the high-water period and low-water period in time spent feeding on fruits, flowers, or arthropods (Table II). During the high-water period, when fruit was most abundant, *Saimiri vanzolinii* consumed more fruit than arthropods ( $N = 52$ ,  $t = 4.859$ ,  $df = 50$ ,  $P < 0.001$ ), a difference not found in the low-water period ( $N = 54$ ,  $t = 0.661$ ,  $df = 52$ ,  $P = 0.510$ ).

**Table 1** Plant species consumed by *Saimiri vanzolinii* and percentage of time spent feeding during low- and high-water periods in 2012–2014 at the Reserva de Desenvolvimento Sustentável Mamirauá

Family	Species	Period	Item	Type	Feeding time (%)
Anacardiaceae	<i>Spondias mombin</i> L.	Low-water	Fruit (*)	Tree	0.5
Annonaceae	<i>Unonopsis floribunda</i> Diels	High-water	Fruit (*)	Tree	2.0
	<i>Xylopia calophylla</i> R.E. Fr.	High-water	Fruit (*)	Tree	0.5
Apocynaceae	<i>Malouetia tamaquarina</i> (Aubl.) A. DC.	High-water	Flower	Tree	1.5
Araceae	<i>Anthurium plowmanii</i> Croat.	Low-water	Fruit	Epiphyte	0.3
Araceae	<i>Bacris brongniartii</i> Mart.	High-water	Fruit	Palm	0.2
Clusiaceae	<i>Garcinia brasiliensis</i> (Mart.)	High-water	Fruit (*)	Tree	0.5
Convolvulaceae	<i>Dicranostyles ampla</i> Ducke	High-water	Fruit	Liana	5.5
	<i>Ipomoea alba</i> L.	High-water	Fruit	Liana	0.2
Dichapetalaceae	<i>Tapura juruana</i> (Ule) Rizzini	High-water	Fruit (*)	Tree	0.5
Dilleniaceae	<i>Dolioscarpus dentatus</i> (Aubl.) Standl.	Low-water	Fruit	Liana	1.3
Dioscoreaceae	<i>Dioscorea latiflora</i> L.	Low-water	Fruit	Liana	1.8
Ebenaceae	<i>Diospyros bullata</i> A.C. Sm.	High-water	Fruit (*)	Tree	0.4
Elaeocarpaceae	<i>Sloanea terniflora</i> (DC.) Standl.	High-water	Fruit (*)	Tree	0.2
Fabaceae	<i>Inga punctata</i> Willd.	Low (1) and high-water (2)	Fruit	Tree	14.2 (1); 4.4 (2)
	<i>Inga</i> sp1 Mill.	High-water	Fruit (*)	Tree	6.7
	<i>Inga</i> sp2 Mill.	High-water	Fruit (*)	Tree	0.9
Icacinaceae	<i>Dendrobangia boliviana</i> Rusby.	High-water	Fruit	Tree	0.9
Lecythidaceae	<i>Eschweilera parvifolia</i> (DC.) Miers	Low (1) and high-water (2)	Flower	Tree	4.6 (1); 0.2 (2)
	<i>Gustavia poeppigiana</i> O. Berg	Low-water	Fruit (*)	Tree	1.0
Loganiaceae	<i>Strychnos guianensis</i> (Aubl.) Mart.	High-water	Fruit	Liana	10.9
Malvaceae	<i>Guazuma ulmifolia</i> Lam.	Low-water	Flower	Tree	0.3

Table 1 (continued)

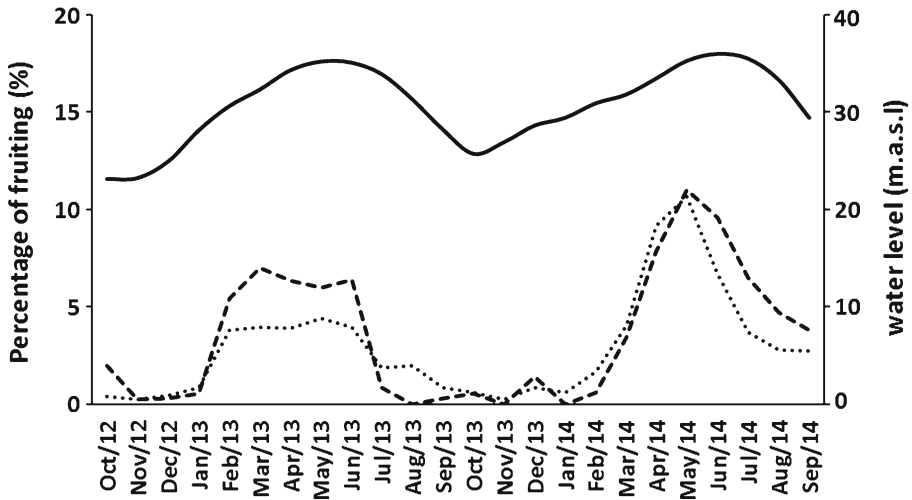
Family	Species	Period	Item	Type	Feeding time (%)
Moraceae	<i>Brosimum lactescens</i> Sw.	Low (1) and high-water (2)	Fruit (*)	Tree	1.0 (1); 0.2 (2)
	<i>Ficus adhatodifolia</i> Schott ex Spreng.	Low (1) and high-water (2)	Fruit (*)	Hemi-epiphyte	0.5 (1); 3.5 (2)
	<i>Ficus amazonica</i> (Miq.) Miq.	High-water	Fruit (*)	Hemi-epiphyte	0.4
	<i>Ficus casapiensis</i> (Miq.) Miq.	Low (1) and high-water (2)	Fruit (*)	Hemi-epiphyte	23.2 (1); 22.2 (2)
	<i>Ficus citrifolia</i> Mill.	High-water	Fruit	Hemi-epiphyte	0.4
	<i>Ficus clusifolia</i> Schott	High-water	Fruit	Hemi-epiphyte	2.7
	<i>Ficus glabrata</i> Kunth	High-water	Fruit	Hemi-epiphyte	0.2
	<i>Ficus mathewsii</i> (Miq.) Miq	Low (1) and high-water (2)	Fruit	Hemi-epiphyte	9.8 (1); 8.2 (2)
	<i>Ficus trigona</i> L. f.	High-water	Fruit	Hemi-epiphyte	2.0
	<i>Ficus</i> sp. L.	Low and high-water	Fruit (*)	Hemi-epiphyte	0.5 (1); 0.5 (2)
Myrtaceae	<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	High-water	Fruit	Tree	1.5
	<i>Eugenia egensis</i> DC.	High-water	Fruit	Tree	0.2
	<i>Eugenia florida</i> DC.	High-water	Fruit (*)	Tree	0.4
	<i>Eugenia lambertiana</i> DC.	Low-water	Fruit	Tree	2.8
Phytolaccaceae	<i>Trichostigma octandrum</i> (L.) H. Walter	High-water	Fruit	Liana	0.5
	<i>Piranhea trifoliata</i> Baill.	High-water	Fruit (*)	Tree	1.5
Picodendraceae	<i>Chomelia tenuiflora</i> Benth.	High-water	Fruit (*)	Tree	0.2
	<i>Psychotria capillacea</i> (Müll. Arg.) Standl.	High-water	Fruit	Tree	0.2
	<i>Banara guianensis</i> Aubl.	High-water	Fruit	Tree	1.1
Sapindaceae	<i>Xylosma benthamii</i> (Tul.) Triana & Planch.	Low (1) and high-water (2)	Fruit	Tree	1.0 (1); 0.4 (2)
	<i>Allophylus amazonicus</i> (Mart.) Radlk	Low-water	Fruit	Tree	0.5
	<i>Paullinia capreolata</i> (Aubl.) Radlk.	High-water	Fruit	Liana	2.0
	<i>Paullinia ingifolia</i> Rich. ex Juss.	High-water	Fruit	Liana	0.5
	<i>Paullinia lethalis</i> L.	High-water	Fruit	Liana	1.5

Table 1 (continued)

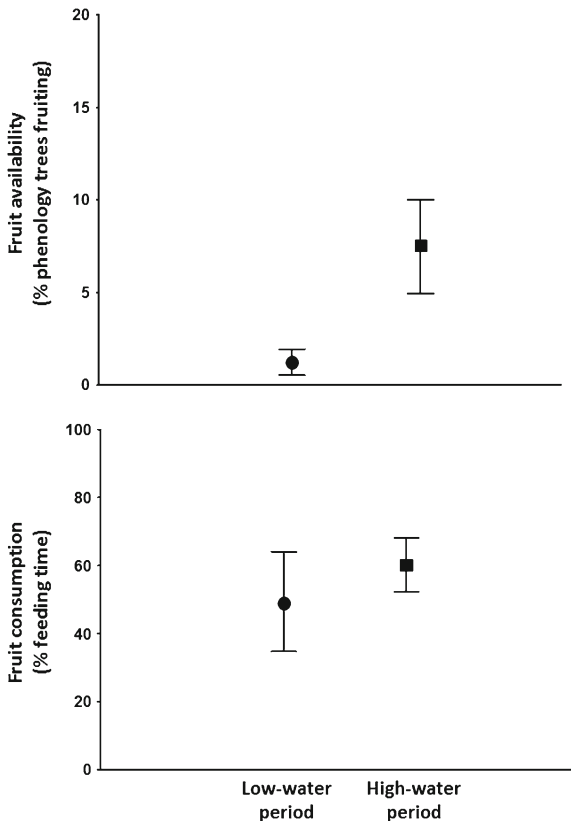
Family	Species	Period	Item	Type	Feeding time (%)
Sapotaceae	<i>Ecclinusa guianensis</i> Eyma	High-water	Fruit (*)	Tree	0.7
	<i>Pouteria glomerata</i> (Miq.) Radlk.	High-water	Fruit (*)	Tree	0.5
	<i>Pouteria proceva</i> (Mart.) K. Hammer	High-water	Fruit	Tree	1.3
Urticaceae	<i>Cecropia latiloba</i> Miq.	Low-water	Fruit (*)	Tree	0.3
	<i>Coussapoa nitida</i> Miq.	Low (1) and high-water (2)	Fruit (*)	Hemi-epiphyte	18.8 (1); 7.6 (2)
	<i>Coussapoa orthoneura</i> Standl.	Low-water	Fruit	Hemi-epiphyte	17.3
Violaceae	<i>Leontia glycyarpa</i> Ruiz & Pav.	High-water	Fruit (*)	Tree	0.4
No identified	Tree no identified	High-water	Fruit	Tree	3.3
	Liana no identified a	High-water	Fruit	Liana	0.5
	Liana no identified b	Low-water	Flower	Liana	0.3

(1) sampled in the low-water period, (2) sampled in the high-water period, (\*) phenology sampled

a and b mean different species of lianas no identified



**Fig. 2** Fruiting phenology during low- and high-water periods in 2012–2014 at the Reserva de Desenvolvimento Sustentável Mamirauá. Solid black line = water level in meters above sea level (m.a.s.l.); dotted line = all tree species sampled ( $N = 205$ ); dashed line = 23 tree species recorded in the diet of *Saimiri vanzolinii*.



**Fig. 3** Mean percentage  $\pm$  SD of trees fruiting and of fruit consumption for the 23 tree species consumed by *Saimiri vanzolinii* in the high-water period and low-water period in 2012–2014, at the Reserva de Desenvolvimento Sustentável Mamirauá, Brazil.

**Table II** Descriptive statistics (means and SD) and the results of *t*-tests comparing the activity budget (% all observations) and feeding time budget for different plant parts and arthropods (% feeding observations) for *Saimiri vanzolinii* between low- and high-water periods in 2012–2014 at the Reserva de Desenvolvimento Sustentável Mamirauá

		Activity budget				Diet			
		Locomotion	Foraging	Feeding	Social	Resting	Flowers	Fruits	Arthropods
Low-water period	<i>N</i>	54	54	54	54	54	54	54	54
	Mean	43.1	25.3	22.6	4.3	4.7	3.3	49.4	43.5
	SD	10.5	11.1	11.5	6.1	6.5	5.1	32.2	31.5
High-water period	<i>N</i>	52	52	52	52	52	52	52	52
	Mean	38.1	24.9	28.0	5.6	3.4	1.2	60.7	36.1
	SD	12.6	10.0	9.5	5.9	6.3	9.8	21.7	19.6
<i>t</i>		227	0.05	2.82	−1.44	1.27	−1.44 <sup>a</sup>	1.67 <sup>a</sup>	−1.07 <sup>a</sup>
<b><i>P</i></b>		<b>0.02</b>	0.96	<b>0.006</b>	0.15	0.21	0.15 <sup>a</sup>	0.97 <sup>a</sup>	0.28 <sup>a</sup>

Bold text indicates significant differences.

*N* number of observation sessions.

<sup>a</sup> Results after adjusting for nonequal variance

## Discussion

Fruiting at RDSM peaked in the high-water period in both years, and this was true among all trees and among the 23 species consumed by *Saimiri vanzolinii*. Flooding peaked at a similar level each year, but the forest remained flooded for longer in 2013, meaning that fruit availability was likely greater in the first year. Although fruit availability was greater during the high-water period, as predicted (prediction 1), there was no difference in the time *S. vanzolinii* spent feeding on fruits between high- and low-water periods (contrary to our second prediction). Fruit abundance did not correlate with the time spent feeding on the 23 consumed species in either season. As predicted, *S. vanzolinii* consumed more fruits than arthropods in the high-water period than in the low-water period (prediction 3), and traveled less in the high-water period than in the low-water (prediction 4). These findings suggest that food selection changed between seasons, and *S. vanzolinii* focused more on fruit in the low-water period, when the resource was less available. These results support the predictions of the ecological constraints model (Chapman and Chapman 2000; Snaith and Chapman 2007).

Seasonal variation in food availability suggests that, during fruit-scarce periods, animals access lower-quality food more frequently than they would in food-rich periods (Hanya *et al.* 2011). Primates adjust their feeding habits to food-scarce periods using different strategies, such as the consumption of fallback foods (Marshall and Wrangham 2007; Marshall *et al.* 2009; Vogel *et al.* 2009). Our results demonstrating consumption of fallback foods by *Saimiri vanzolinii* during the low-water period are similar to those reported for *Hylobates albibarbis* and for *Pongo pygmaeus wurmbii*, which ate fallback foods, i.e., figs, lianas and unripe fruits, during fruit-scarce periods (Vogel *et al.* 2009). *Macaca fuscata* was also reported to have changed their diet,

consuming fallback foods during the fruit-scarce periods, including leaves and barks, instead of figs (Hanya 2004), as we observed for *S. vanzolinii*.

In addition to the 23 species we monitored, *Saimiri vanzolinii* consumed fruits from another 33 woody plant species with DBH <10 cm, including lianas and important rare trees, besides *Ficus* species. Our lack of data for these species might have obscured seasonal foraging differences. For example, we did not sample most fig species, but throughout the year these fruits were important species in the monkey's diet. Figs play an important role in the diet of several primates, especially during periods of food shortage, being considered fallback foods (Marshall and Wrangham 2007; Marshall *et al.* 2009). *S. vanzolinii* often consumed figs in both seasons, so they are likely to play such a role for this species, as reported for *S. boliviensis* (Mitchell 1990; Terborgh 1983).

*Saimiri vanzolinii* consumed more fruits than arthropods in the high-water period, although it is not clear if this result is related to higher fruit availability or to preference. We did not sample arthropods, but their availability in many Amazonian sites is constant throughout the year (Pearson and Derr 1986; Penny and Arias 1982; Stone 2007a). Most primates eat some ripe fruit, i.e., high-quality food in terms of easily digestible carbohydrates (Hawes and Peres 2014a, b); however, they also need to acquire protein, which can be obtained from arthropods (Deluycker 2012). Although fruit availability differed between seasons, *S. vanzolinii* consumed more fruits than insects in our study and it appears that they used arthropods primarily as a supplementary resource. In general, arthropods are more dispersed than fruits, and primates use a different foraging strategy to access them (Terborgh 1983). In contrast, other Neotropical species (*Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capuccinus*) in Central America did not change their feeding behavior seasonally, probably because most of the plants they consume did not vary in availability by season (Chapman 1988). It is likely that the availability of different resources used by *S. vanzolinii* across time explains our findings, and we hope that future studies addressing seasonal variation in fruit availability and arthropod biomass will help clarify this pattern.

*Saimiri vanzolinii* spent more time traveling and less time feeding during the low-water period than during the high-water period. Time spent traveling can be affected by distribution of feeding resources, mates, and sleeping sites, as animals need to travel further when availability of such resources is lower (Holyoaka *et al.* 2008; Mueller and Fagan 2008). Our results suggest *S. vanzolinii* maintained high fruit consumption despite the lower abundance of fruit during the low-water period by traveling longer distances between resources. However, we found no significant correlation between the time spent traveling and fruit abundance in either season. The same traveling pattern has been observed in *S. boliviensis*, which travel further in the dry season (lean period) to visit important resources such as large fig trees (Terborgh 1983). In contrast, *S. collinsi*, in Eastern Amazonia, did not show seasonal differences in travel time, probably because they used a habitat with a high concentration of an important arthropod in their diet (Stone 2007a). Our results also differ from those for *Callithrix penicillata*, which dedicated more time to locomotion during the food-rich period, and consumed more arthropods than fruits during the fruit-scarce period (Vilela and Faria 2004).

The unknown home range of groups of *Saimiri vanzolinii* at RDSM and difficulty in sampling small agile monkeys in flooded forests meant we were not able to recognize groups individually. Thus, we could not ensure that we sampled different groups on the different trails and our results must be treated with caution because of the possibility

that our data are pseudoreplicated, i.e., the sample sizes of 54 for the low-water period and 52 for the high-water period may effectively be smaller.

*Saimiri vanzolinii*'s range is within a protected area and the population is currently not threatened by human activity. However, although a sustainable forest management plan is in place at RDSM, illegal logging still occurs (Queiroz and Peralta 2010), and, if this logging expands, it could be of serious concern for the conservation of *S. vanzolinii*. One of the overexploited timber species (*Piranhea trifoliata*) is an important food species for *S. vanzolinii*. This should be considered in conservation plans at RDSM. Furthermore, climate models predict changes in Western Amazonia, with higher and longer flooded periods (IPCC 2014; Marengo and Espinoza 2015), representing a potential impact on flooding patterns, which could lead to changes in phenology patterns and loss of habitat for *S. vanzolinii*. Therefore, we should continue to monitor the population of *S. vanzolinii* and its food resources to ensure that habitat changes do not threaten its future.

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## References

- Araujo, M. (2014). Ecologia alimentar de *Saimiri sciureus* cassiquiarensis (Lesson, 1840) (Primates, Cebidae) em florestas de várzea da Amazônia Central Brasileira. In *MSc thesis*. Federal do Pará and Museu Paraense Emílio Goeldi: Universidade.
- Ayres, J. M. (1993). *As matas de várzea do Mamirauá: Médio Rio Solimões*. Brasília: Sociedade Civil Mamirauá/CNPq.
- Boinski, S. (1987). Habitat use by squirrel monkey (*Saimiri oerstedii*) in Costa Rica. *Folia Primatologica*, 49, 151–167.
- Boinski, S. (1988). Sex differences in the foraging behaviour and substrate use of squirrel monkeys in a seasonal habitat. *Behavioural Ecology and Sociobiology*, 23, 177–186.
- Boinski, S. (1999). The social organization of squirrel monkeys: Implications for ecological models of social evolution. *Evolutionary Anthropology*, 8, 101–112.
- Boubli, J. P., & Rylands, A. B. (2008). *The IUCN Red List of Threatened Species*, 2008. doi:10.2305/IUCN.UK.2008.RLTS.T19839A9023022.en Accessed 10 Mar 2017.
- Boyle, B., Hopkins, N., Lu, Z., Garay, J. A. R., Mozzherin, D., et al (2013). The taxonomic name resolution service: An online tool for automated standardization of plant names. *BMC Bioinformatics*. doi:10.1186/1471-210.
- Chapman, C. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29, 177–194.
- Chapman, C. A., & Chapman, L. J. (2000). Determinants of group size in social primates: The importance of travel costs. In S. Boinski & P. A. Garber (Eds.), *On the move: How and why animals travel in groups* (pp. 24–42). Chicago: University of Chicago Press.
- Deluycker, A. M. (2012). Insect prey strategies in *Callicebus oenanthe* in northern Peru. *American Journal of Primatology*, 74, 450–461.
- Di Fiore, A., & Campbell, C. J. (2005). Contemporary issues in ecology, behavior, and evolution of the Ateline primates. *International Journal of Primatology*, 26, 995–997.

- Furch, K. (1984). Water chemistry of the Amazon basin: The distribution of chemical elements among freshwaters. In H. Sioli (Ed.), *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin* (pp. 167–199). Dordrecht: W. Junk.
- Hanya, G. (2004). Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *International Journal of Primatology*. doi:10.1023/B:IJOP.0000014645.78610.32.
- Hanya, G., Stevenson, P., van Noordwijk, M., Wong, S. T., et al (2011). Seasonality in fruit availability affects frugivorous primate biomass and species richness. *Ecography*. doi:10.1111/j.1600-0587.2010.06775.x.
- Haugaasen, T., & Peres, C. A. (2005). Tree phenology in adjacent Amazonian flooded and unflooded forests. *Biotropica*, 37(4), 620–630.
- Hawes, J., & Peres, C. A. (2014a). Ecological correlates of trophic status and frugivory in neotropical primates. *Oikos*. doi:10.1111/j.1600-0706.2013.00745.x.
- Hawes, J., & Peres, C. A. (2014b). Fruit–frugivore interactions in Amazonian seasonally flooded and unflooded forests. *Journal of Tropical Ecology*. doi:10.1017/S0266467414000261.
- Hawes, J., & Peres, C. A. (2016). Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. *Biotropica*. doi:10.1111/btp.12315.
- Hemingway, C. A., & Bynum, N. (2012). The influence of seasonality on primate diet and ranging. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 55–104). Cambridge: Cambridge University Press.
- Holyoaka, M., Casagrandib, R., Nathanc, R., Revillad, E., & Spiegelc, O. (2008). Trends and missing parts in the study of movement ecology. *PNAS*. doi:10.1073/pnas.0800483105.
- Instituto de Desenvolvimento Sustentável Mamirauá (2015). *Banco de dados fluviométrico da Reserva de Desenvolvimento Sustentável Mamirauá*. <http://mamiraua.org.br/pt-br/pesquisa-e-monitoramento/monitoramento/fluviometrico/>. Accessed 15 Sept 2015.
- IPCC (2014). Climate change 2014: Synthesis report. In R. K. Pachauri & L. A. Meyer (Eds.), *Contribution of working groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change* (pp. 2–26). Geneva: Intergovernmental Panel on Climate Change.
- Janzen, D. H. (1967). Synchronization of sexual reproduction of trees within the dry season in central America. *Evolution*, 21, 620–637.
- Junk, W. J. (1989). Flood tolerance and tree distribution in central Amazonian floodplains. In L. B. Holm-Nielsen, I. C. Nielsen, & H. Balslev (Eds.), *Tropical forests: Botanical dynamics, speciation and diversity* (pp. 47–64). London: Academic Press.
- Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. In D. P. Dodge (Ed.), *Proceedings of international large river symposium (LARS)* (pp. 110–127). Toronto: Canadian Special Publication of Fisheries and Aquatic Sciences.
- Junk, W. J., Piedade, M. T. F., Schöngart, J., & Wittmann, F. (2012). A classification of major natural habitats of Amazonian white-water river floodplains (várzeas). *Wetlands Ecology and Management*, 20(6), 461–475.
- Klammer, G. (1984). The relief of the extra-Andean Amazon basin. In H. Sioli (Ed.), *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin* (pp. 49–83). Dordrecht: W. Junk.
- Lima, E. M., & Ferrari, F. F. (2003). Diet of a free-ranging group of squirrel monkeys (*Saimiri sciureus*) in eastern Brazilian Amazonia. *Folia Primatologica*. doi:10.1159/000070648.
- Marengo, J., & Espinoza, J. C. (2015). Extreme seasonal drought and flood in Amazonia: Cause, trend and impact. *International Journal of Climatology*, doi:10.1002/joc.4420.
- Marsh, L. K. (2014). A taxonomic revision of the saki monkeys, *Pithecia* Desmarest, 1804. *Neotropical Primates*, 21(1), 1–163.
- Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*. doi:10.1007/s10764-007-9218-5.
- Marshall, A. J., Boyko, C. M., Feilen, K. L., Boyko, R. H., & Leighton, M. (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*. doi:10.1002/ajpa.21082.
- Melack, J. M., & Hess, L. L. (2010). Remote sensing of the distribution and extent of wetlands in the Amazon basin. In W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, & P. Parolin (Eds.), *Amazonian floodplain forests: Ecophysiology, biodiversity and sustainable management* (pp. 43–59). Heidelberg: Springer.
- Mendoza, I., Peres, C. A., & Morellato, L. P. C. (2016). Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. *Global and Planetary Change*. doi:10.1016/j.gloplacha.2016.12.001.
- Mitchell, C. L. (1990). *The ecological basis for female social dominance: A behavioral study of the squirrel monkey*. PhD thesis, Princeton University.

- Mueller, T., & Fagan, W. F. (2008). Search and navigation in dynamic environments: From individual behaviors to population. *Oikos*. doi:10.1111/j.0030-1299.2008.16291.x.
- Paim, F. P., & Queiroz, H. L. (2009). Diferenças nos parâmetros acústicos das vocalizações de alarme das espécies de *Saimiri* Voigt, 1831 (Primates, Cebidae) na floresta de várzea – Reserva Mamirauá. *Uakari*, 5, 49–60.
- Paim, F. P., Silva Júnior, J. S., Valsecchi, J., Harada, M. L., & Queiroz, H. L. (2013). Diversity, geographic distribution and conservation of squirrel monkeys, *Saimiri* (primates, Cebidae), in the floodplain forests of central Amazon. *International Journal of Primatology*. doi:10.1007/s10764-013-9714-8.
- Paim, F. P., Silva Júnior, J. S., & Queiroz, H. L. (2015). *Avaliação do risco de extinção de Saimiri vanzolinii Ayres, 1985 no Brasil*. ICMBio: Processo de avaliação do risco de extinção da fauna brasileira <http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/estado-de-conservacao/7268-mamiferos-saimiri-vanzolinii-macaco-de-cheiro-de-cabeça-preta.html>. Accessed 23 Nov 2016.
- Parolin, P., Wittmann, F., & Schöngart, J. (2011). Tree phenology in Amazonian floodplain forests. In W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, & P. Parolin (Eds.), *Amazonian floodplain forests: Ecophysiology, biodiversity and sustainable management* (pp. 105–126). Dordrecht: Springer.
- Pearson, D. L., & Derr, J. A. (1986). Seasonal patterns of lowland forest floor arthropod abundance in southeastern Peru. *Biotropica*, 18(3), 244–256.
- Penny, N. D., & Arias, J. R. (1982). *Insects of an Amazon forest*. New York: Columbia University Press.
- Queiroz, H. L., & Peralta, N. (2010). Protected areas in the Amazonian Várzea and their role in its conservation: The case of Mamirauá sustainable development reserve (MSDR). In W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, & P. Parolin (Eds.), *Amazonian floodplain forests: Ecophysiology, biodiversity and sustainable management* (pp. 465–483). Springer: Heidelberg.
- Rabelo, R. M., Silva, F. E., Vieira, T., Ferreira-Ferreira, J., Paim, F. P., et al (2014). Extension of the geographic range of *Ateles chamek* (primates, Atelidae): Evidence of river-barrier crossing by an amazonian primate. *Primates*. doi:10.1007/s10329-014-0409-3.
- Ramalho, E. E., Macedo, J., Vieira, T. M., Valsecchi, J., Calvimontes, J., et al (2009). Ciclo hidrológico nos ambientes de várzea da Reserva de Desenvolvimento Sustentável Mamirauá – médio Rio Solimões, período de 1990 a 2008. *Uakari*, 5(1), 61–87.
- van Schaik, C. P., Terborgh, J. W., & Wright, S. J. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24, 353–377.
- Schöngart, J., Piedade, M. T. F., Ludwigshausen, S., Horna, V., & Worbes, M. (2002). Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology*, 18, 581–597.
- Snaith, T. V., & Chapman, C. A. (2007). Primate group size and socioecological models: Do folivores really play by different rules? *Evolutionary Anthropology*. doi:10.1002/evan.20132.
- Stone, A. (2006). Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (*Saimiri sciureus*). *Ethology*. doi:10.1111/j.1439-0310.2005.01121.x.
- Stone, A. (2007a). Responses of squirrel monkeys to seasonal changes in food availability in an eastern Amazonian forest. *American Journal of Primatology*. doi:10.1002/ajp.20335.
- Stone, A. (2007b). Ecological risk aversion and foraging behaviors of juvenile squirrel monkeys (*Saimiri sciureus*). *Ethology*. doi:10.1111/j.1439-0310.2007.01377.x.
- Terborgh, J. (1983). *Five new world primates: A study in comparative ecology*. Princeton: Princeton University Press.
- Valsecchi, J. (2005). Diversidade de mamíferos e uso da fauna nas Reservas de Desenvolvimento Sustentável Mamirauá e Amaná – Amazonas – Brasil. In *MSc thesis*. Federal do Pará and Museu Paraense Emílio Goeldi: Universidade.
- Vilela, S. L., & Faria, D. S. (2004). Seasonality of the activity pattern of *Callithrix penicillata* (primates, Callitrichidae) in the cerrado (scrub savanna vegetation). *Brazilian Journal of Biology*. doi:10.1590/S1519-69842004000200023.
- Vogel, E. R., Haag, L., Mitra-Setia, T., van Schaik, C. P., & Dominy, N. J. (2009). Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical Anthropology*. doi:10.1002/ajpa.21119.
- Wittmann, F., Anhof, D., & Junk, W. J. (2002). Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *Journal of Tropical Ecology*. doi:10.1017/S0266467402002523.
- Wittmann, F., Junk, W. J., & Piedade, M. T. F. (2004). The várzea forests in Amazonia: Flooding and the highly dynamic geomorphology interact with natural forest succession. *Forest Ecology and Management*, doi:10.1016/j.foreco.2004.02.060.
- Wittmann, F., Schöngart, J., Queiroz, H. L., Wittmann, A. O., Conserva, A. S., et al (2009). The Amazon floodplain demonstration site: Sustainable timber production and management of central Amazonian white-water floodplains. *Ecology and Hydrobiology*. doi:10.2478/v10104-009-0038-4.

- Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*. doi:10.1093/beheco/aru183.
- Yang, L. H., Bastow, J. L., Spence, K. O., & Wright, A. N. (2008). What can we learn from resource pulses? *Ecology*. doi:10.1890/07-0175.1.