Eat the fruit earlier: Sakis (*Pithecia chrysocephala*) show enhanced temporal fruit resource access compared with squirrel monkeys (*Saimiri sciureus*) in an urban forest fragment in Brazil

Running title: Advantages of the saki feeding system

Makiko Take[1,2†1]*, Takakazu Yumoto[1], Adrian A. Barnett[2,3], Kota Onizawa[4‡], Wilson R. Spironello[2]

[1]Primate Research Institute, Kyoto University, Inuyama, Aichi, Japan

[2]Grupo de Pesquisa de Mamíferos Amazônicos, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil

[3]Animal and Agricultural Sciences, Hartpury University, Gloucester, England

[4]Wildlife Research Center, Kyoto University, Kyoto, Japan

[†]Current affiliation: Wildlife Research Center, Kyoto University, Kyoto, Japan

[‡] Current affiliation: Field Science Center for Northern Biosphere, Hokkaido University, Uryu, Hokkaido, Japan

***Correspondence:**

Makiko TAKE

Kanrin, Inuyama 484-8506, Aichi, Japan

take.makiko.77a@gmail.com

+81-90-8258-0742

Abstract

Fruit availability experienced by different primate species is likely to vary due to species-specific fruit use, even within the same habitat and timeframe. Pitheciines, primates of the subfamily *Pitheciinae*, particularly favor the seeds of unripe fruits. Researchers consider this dietary characteristic an adaptation to increase access to fruit resources. However, the relative advantages of pitheciines over sympatric non-pitheciine non-seed-eating primates regarding species-specific fruit availability is not well studied. In a 26-ha forest within the city of Manaus, Amazonian Brazil, we assessed the wild-food feeding behavior of free-ranging groups of golden-faced sakis (*Pithecia chrysocephala*) and sympatric common squirrel monkeys (*Saimiri sciureus*). We hypothesized that sakis would have greater and more consistent access to wild fruit due to 1) a wider variety of fruit species in their diet, and 2) longer consumption periods per fruit species. We recorded the plant species, part (pulp or seed), and developmental stage (ripe or unripe) of wild fruit consumed by both species. We also conducted monthly fruit censuses of 1,000 trees and vines to estimate overall wild fruit abundance. As an indicator of fruit availability, we calculated the proportion of available fruiting trees and vines for each primate species separately based on their observed diet. Throughout the year, the proportion of available trees and vines was significantly higher and more temporally stable for sakis than for squirrel monkeys. This was because sakis used shared fruit species longer than squirrel monkeys by consuming both ripe and unripe fruit. Although sakis had a broader fruit repertoire than squirrel monkeys, it did not contribute to the higher fruit availability. Thus, the fruit feeding system of sakis identifies aspects of a niche that is less restricted in the timing of fruit consumption, which led to a relative advantage in fruit availability.

Keywords

Seed predator, fruit availability, fruit choice, South American primate, niche partitioning

Abbreviations

INPA: Instituto Nacional de Pesquisas da Amazônia

DBH: diameter at breast height

Introduction

Fruit resources are used by the majority of tropical forest vertebrates, including primates (Fleming et al., 1987, Fleming & Kress, 2011; Fuzessy et al., 2021; Hawes & Peres, 2013). Fruit availability affects many aspects of primate behavior, including feeding, ranging, sociality, and reproduction (van Schaik & Brockman, 2005; Lambert & Rothman, 2015). Therefore, adaptations enhancing access to fruit resources offer evolutionary advantages to primates.

Fruit preference varies among primate species (Izawa, 1975; Guillotin et al., 1994; Martins, 2008). As composites, fruits consist of pulp and seed, with different mechanical, chemical, and nutritional properties depending on their developmental stage (Brady, 1987; Janzen, 1983). A single fruit species offers several resources that may only be accessible to a subset of animal species. Therefore, a distinction can be drawn between "fruit abundance" (the estimated number of individual fruits growing on trees in the habitat) and "fruit availability" (the fruit a specific species is capable of consuming based on their morphology, feeding behavior, and the presence of other species in the same habitat). While the abundance of a specific fruit in a habitat remains consistent, the fruit availability experienced by specific species is likely to differ.

Pitheciines, primates of the subfamily *Pitheciinae* (*Cacajao*, *Chiropotes*, and

Pithecia; endemic to the Amazonian and Guianan forests), exhibit unique fruit use. Their morphological traits and feeding behavior allow them to consume both the pulp and seeds of fruits, including unripe ones (Bowler & Bodmer, 2011; Happel, 1982; Norconk, 1996; Peres, 1993; van Roosmalen et al., 1988). Their specialized dental and jaw structure enables them to break open hard pericarps and seed coats (Kinzey, 1992; Ledogar et al., 2018). This adaptation broadens their fruit options beyond the soft and juicy fruits favored by other primates (Charpentier et al., 2015; Norconk & Veres, 2011; Kinzey and Norconk, 1990). Additionally, by incorporating both unripe and ripe fruits into their diet, they can extend the availability of each fruit species (Palminteri, 2012). Due to these characteristics, pitheciines possibly enjoy relatively higher fruit availability than sympatric non-seed-eating primate, but it has not been directly examined.

Sakis (genus *Pithecia*), the smallest pitheciine, are widespread in northern South America and often occur sympatrically with many other primate species (Happel, 1982; Peres, 1991). Eastern and Central Amazonian sakis (*P. pithecia* and *P. chrysocephala*) are known to use the middle to lower layers of forests (Mittermeier & van Roosmalen, 1981; Oliveira et al., 1985; Setz et al., 2013), where they frequently coexist with squirrel monkeys (genus *Saimiri*) (Rowe & Myers, 2016; Mittermeier & van Roosmalen, 1981; Pinheiro et al., 2013). Squirrel monkeys are insectivore-frugivores, and more than half of their diet consists of fruit or flowers (Lima & Ferrari, 2003). Sakis often chew and destroy the seeds of fruit (Setz 1993, Norconk & Setz, 2013; Norconk, 2020), while squirrel monkeys, like many frugivorous primates, swallow or spit them out (Take, 2017).

In this study, we investigated the feeding habits of golden-faced sakis (*Pithecia chrysocephala*) and common squirrel monkeys (*Saimiri sciureus*) in a forest fragment in Manaus, Amazonian Brazil. Using interspecific comparisons, we examined the hypotheses that sakis have greater access to wild fruit than sympatric non-seed-eating squirrel monkeys due to: 1) a wider variety of fruit species in sakis' diet, and 2) longer consumption periods per fruit species in sakis. To ensure the validity of our comparisons, we assessed whether the primate species at the study site consumed similar amounts of the regularly provided supplemental food. We investigated the wild fruit choice of the two primate species, including data on the species, part (pulp or seed) and developmental stage of the fruit (unripe or ripe). As an indicator of fruit availability, we calculated the monthly proportion of available fruiting trees or vines for each primate species based on the observed fruit choices and compared them.

Methods

Ethics statement

The study protocol complied with the Guidelines for Field Research established by the Ethics Committee of the Primate Research Institute, Kyoto University, Japan, as well as the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Study site

The study was conducted at Campus I of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Amazonas, Brazil (3°09′ S, 59°99′ W) (Figure 1). The study site is a 26-ha fragment of secondary lowland Amazonian *terra firme* forest enclosed on all sides by tarmacked roads. The site houses four species of free-ranging primates: pied tamarins (*Saguinus bicolor*), common squirrel monkeys, golden-faced sakis, and owl monkeys (*Aotus* cf. *nigriceps*). The study site is also inhabited by non-primate frugivores, such as iguanas, opossums, and various birds, including macaws and toucans. Mean annual precipitation in Manaus was 3001 mm over the past 30 years (Climate-data.org, n.d.). Rainfall is highly seasonal, with a dry season from June to November, and a rainy season from December to May. Monthly precipitation during the study period followed this pattern, with relatively more rain in September and October and less rain in November and December (Instituto Nacional de Meteorológia, n.d.)

(Figure 2a). The monkeys have been provided with supplemental food on a daily basis since 1995 as part of the Bosque da Ciência (“grove/forest of science”) environmental education initiative under the leadership of Dr. Marc van Roosmalen. At the time of this study, eight provisioning tables accessible to all monkeys were distributed across campus (Figure 1). Six of these tables provided 1 kg of banana, 500 g of papaya, and 300 g of pineapple pulp (in 5 g pieces), and two tables provided 100 g of coconut flesh (in 1 g pieces). The contents and volume of the food (provided at 07:00 AM daily) remained constant throughout the study period.

Vegetation survey

We established 16 transects (5 m wide) at 50 m intervals (Figure 1). The maximum length of each transect was 200 m, excluding buildings, roads, and ponds, to maximize sampling area size. The transects covered a total length of 2844 m and an area of 1.42 ha, accounting for approximately 5.5% of the total campus area. As monkeys at the study site often eat fruits from trees with a diameter at breast height (DBH) $<$ 10 cm (e.g., *Siparuna guianensis* or *Leonia cymosa*), we tagged and identified every tree and vine with a DBH ≧ 5 cm within the transects. We measured DBH with a tape measure. Basal area (cross-sectional area at breast height) was calculated based on DBH. Plant species were identified with the assistance of Mr. José Ferreira Ramos, a plant specialist at INPA.

Fruit census

To estimate wild fruit availability, we randomly selected 1000 tagged trees and vines, regardless of whether they were used by monkeys. Each month, from January 2019 to February 2020, we recorded the presence or absence of fruits as well as their developmental stage (ripe or unripe, based on external color and any notable changes between surveys).

Study groups

We studied two groups of golden-faced sakis and one group of common squirrel monkeys. Saki Group A comprised 9 individuals: 4 adult males, 2 adult females, and 3 female juveniles. At the beginning of the study, Group B had 13 individuals: 5 adult males, 3 adult females, 3 juvenile males, and 2 juvenile females; however, 1 adult male left in March 2019, and 1 female was born in October 2019. We defined an “adult” saki as an individual older than 4 years. The squirrel monkey group comprised approximately 50 individuals. Their group composition was unclear because of the difficulty in determining the age and sex of young individuals. The two saki groups used the northern and southern halves of the forest, respectively, while the squirrel monkey group used the entire campus area (Take, 2017). All three groups were well-accustomed to the presence of observers at the beginning of the study.

Observation of feeding behavior

We conducted full-day observations of each monkey group for 3–4 days per month, from March 2019 to February 2020. We recorded the feeding activities of all visible individuals (except dependent infants) in 10-min intervals via the instantaneous group scan sampling procedure (Altmann, 1974). During the observation, the observer tried to be at the center of the focal group to scan as many individuals as possible. Foods eaten were categorized as follows: provisioned foods, wild fruit pulp, wild fruit seeds, unknown parts of wild fruits, flowers, leaves, insects, and “other” (including plant stems, termite nests, and mother’s milk). For wild fruits containing seeds < 1 mm in size, such as *Cecropia*, we assumed that the pulp was consumed. For wild fruits that include pulp and seeds, the developmental stage (ripe or unripe) of consumed fruit was also recorded.

Data analysis

We examined daily diet composition in two ways: by comparing provisioned food versus wild food, and by considering the composition of wild food only. To avoid overrepresenting highly visible feeding behaviors, such as feeding on provisioned foods, we performed all calculations as follows: First, for each scan in which feeding was recorded, we calculated the percentage of each food category by dividing the number of individuals eating the food by the total number of feeding individuals in the scan. Second, for each food category, we calculated the average percentage per scan per day.

To assess the dependency of each group on provisioned foods, we conducted a one-way ANOVA using the daily percentage of provisioned foods consumed per group.

To compare the number of wild fruit species used between primate species while addressing the variation in sampling effort, we constructed diversity accumulation (rarefaction) curves using the R package iNEXT (ver. 2.0.20; Hsieh et al., 2016) with extrapolation and 95% confidence intervals based on individual abundance data (Chao et al., 2014). To account for interspecific differences in fruit dependency, we used the number of feeding records on wild fruits as the unit for the x-axis instead of the total number of feeding records. Following Chao et al. (2014), we considered the extrapolation endpoint to be double the smallest sample size or equal to the maximum sample size, whichever was greater. We considered the diversity of wild fruit species used to be significantly different when the confidence intervals did not overlap within the range of extrapolation.

We compared the composition of the consumed part (seed or pulp) and developmental stage (unripe or ripe) of shared wild fruit species between the primate species using a chi-square test of independence based on the number of feeding records in each category (i.e., ripe pulp, ripe seed, unripe pulp, or unripe seed). We then conducted a residual analysis to identify categories with a higher or lower value than anticipated. To compare the periods when the monkeys shared wild fruit species, we used an exact Wilcoxon signed-rank test with the consumption period (months) for each fruit species as the dependent variable ($N = 43$ species).

To compare wild fruit availability between the two primate species, we calculated the proportion of available fruiting trees and vines based on their observed diets. First, we compiled a list of wild fruits eaten, including the species, parts (pulp or seed), and developmental stage (unripe or ripe). The proportion of available feeding trees and vines was calculated for each month by dividing the number of trees and vines bearing fruit by the total number of trees and vines, while accounting for the developmental stage of the fruit (ripe or unripe). For example, if monkeys ate only the ripe fruits of plant species A, we calculated the proportion of trees/vines bearing ripe fruits. If monkeys ate both unripe and ripe fruits, we calculated the proportion of trees/vines bearing fruit at either of the developmental stages (ripe or unripe). Calculations included all wild fruit species that were used once or more. We used the Exact Wilcoxon signed-rank test to compare groups, with the monthly proportion of available feeding trees and vines as the dependent variable (N = 14). In addition, as an indicator of the consistency of fruit availability, we calculated the coefficient of variation (CV) by dividing the mean by the standard deviation for the monthly proportion of fruiting trees and vines (N = 14) for sakis and squirrel monkeys. The R package cvequality (ver. 0.1.3; Marwick & Krishnamoorthy, 2019) was used to test for differences in the CV between primate species. Statistical significance was set at $p < 0.05$. Data are presented as the mean ± SD.

Results

In the vegetation survey, we recorded 1,807 individual trees/vines, which belonged to 223 plant species within 156 genera and 58 families (Table S1). Fabaceae dominated in terms of species and basal area, whereas Arecaceae dominated in terms of the number of individual trees (Table S1). *Euterpe oleracea* (Arecaceae) had the greatest number of individual trees (N = 405), followed by *Siparuna guianensis* (Siparunaceae, N

= 68), *Inga alba* (Fabaceae, N = 44), *Attalea maripa* (Arecaceae, N = 38), and *Guatteria scytopylla* (Annonaceae, N = 37).

Regarding observation of feeding behavior, we conducted 4,523 scans of the saki groups (Group A, N = 2,345; Group B, N = 2,178). On average, 4.9 individuals were observed at each scan (Group A, 4.6 individuals; Group B, 5.3 individuals).We collected 5,456 feeding records of sakis (Group A, N = 2,563; Group B, N = 2,893), in which we identified 98% of the food categories (97% in Group A, 99% in Group B). For squirrel monkeys, we conducted 2,643 scans. On average, 5.6 individuals were observed during each scan. We collected 3,737 feeding records of squirrel monkeys, in which we identified 99.9% of the food categories.

Use of provisioned foods

All monkey groups visited the provisioning tables daily, apart from one day where saki Group A did not visit the tables. Despite this, the mean percentage of provisioned foods in all group diets was < 13% (saki Group A, 10.9 ± 5.91%, N = 40 d; saki Group B, 12.8 ± 5.15%, N = 38 d; squirrel monkeys, 11.4 ± 4.29%; N = 38 d). There were no significant differences in dependency on provisioned foods among the monkey groups (ANOVA: F = 1.36, p = 0.26). However, there were distinct interspecific differences in the preference for provisioned foods. Sakis consumed all coconut flesh pieces first before eating fruit pulp. On average, coconut flesh accounted for 40.3% of the provisioned foods consumed by sakis (Group A, 43.9 ± 30.0%; Group B, 36.7 ± 18.0%). The squirrel monkeys only used the provisioned fruit pulp (i.e., bananas, papayas, and pineapples) and never used the coconut flesh.

Wild fruit use

Excluding the provisioned foods, the two primate species showed different dietary compositions (Table 1). The use of wild fruits (pulp and seeds) accounted for 80.9% of the sakis' diet (80.7% in Group A, 81.1% in Group B) and 41.2% of the squirrel monkeys' diet (Table 1). Sakis used 148 fruit species (76 genera in 37 families), and squirrel monkeys used 77 fruit species (52 genera in 31 families) (Table 2). The primates shared 43 fruit species (Table 2).

Accounting for differences in sampling effort (Figure 3), sakis fed from significantly more wild fruit species than squirrel monkeys and used more non-shared species (sakis, N = 105 spp.; squirrel monkeys, N = 34 spp.). Non-shared species used by sakis included *Attalea maripa* and *Oenocarpus bacaba* palms, the ripe pulp of which was their most eaten wild fruit (Table 2).

Even within the same wild fruit species, the composition of the developmental stage and part consumed varied between primate species ($\chi^2 = 1{,}111.7$, df = 3, $p < 0.01$, Cramer's V = 0.629) (Figure 4). Squirrel monkeys mostly used ripe fruits (pulp = 92.5%, seeds = 6.9%) while sakis ate significantly more unripe seeds (43.2%, residual analysis, adjusted residual = 25.812, $p < 0.001$) and unripe pulp (1.8%, adjusted residual = 3.241, $p < 0.001$) than expected. Sakis ate significantly less ripe pulp than expected (25%, adjusted residual = 32.859, $p < 0.001$) (Figure 4).

Sakis used the shared wild fruit species for a longer period than squirrel monkeys (Exact Wilcoxon signed-rank test, V = 486, $p < 0.001$, N = 43) (Figure 5, Table S2).

Comparison of wild fruit availability

Of the 182 wild fruit species used by the monkeys, we calculated the fruit availability (i.e., proportion of available fruiting trees and vines) of 56 species included in the fruit census (Table 2, Figure 6). Among them, 31 species were shared, 20 species were used only by sakis, and five species were used only by squirrel monkeys (Table 2). The proportion of available fruiting trees and vines was higher for sakis than for squirrel monkeys throughout the year (Exact Wilcoxon signed-rank test, V = 105, $p < 0.001$, N = 14) (Figure 6a). The CV was significantly higher for squirrel monkeys than for sakis

(sakis: 0.176; squirrel monkeys: 0.433; MSLRT = 7.981; $p = 0.005$) (Figure 6a), indicating that the proportion of available fruiting trees and vines was more stable for sakis during the study period. These results were consistent with that of the shared fruit species in terms of the proportion of available fruiting trees and vines (Exact Wilcoxon signed-rank test, V = 105, $p < 0.001$, N = 14) and CV (saki: 0.169, squirrel monkey: 0.519, MSLRT = 11.699, $p < 0.001$) (Figure 6b). On the other hand, for non-shared fruit species, there were no differences between the two primate species in the proportion of available fruiting trees and vines (Exact Wilcoxon signed-rank test, V = 42, $p = 0.839$, N = 14) (Figure 6c) and CV (sakis: 0.454; squirrel monkeys: 0.377; MSLRT = 0.315; $p = 0.575$) (Figure 6c).

Discussion

In this study, we hypothesized that sakis would have greater access to wild fruit than squirrel monkeys would, due to 1) a wider variety of fruit species in their diet, and 2) a longer consumption period per fruit species. Our data supported hypothesis 2 but did not support hypothesis 1. By consuming wild fruits at both unripe and ripe stages (Table 2), sakis used shared fruit species earlier and over a longer period than squirrel monkeys (Figures 5 and 6b). As a result, the proportion of available fruiting trees and vines was significantly higher and more temporally stable for sakis than for squirrel monkeys (Figure 6a). Sakis used a wider variety of fruit species than squirrel monkeys (Figure 3), but it did not contribute to the higher fruit availability (Figure 6c).

Effect of provisioned foods

More than 85% of the daily diet of sakis and squirrel monkeys at this study site consisted of wild foods. For both primate species, the composition of the wild foods resembled those reported in non-provisioned conditions (Table 1; Norconk & Conklin-Brittain, 2004; Zimbler-DeLorenzo & Stone, 2011). Furthermore, squirrel monkeys in this study used 77 wild fruit species, surpassing previous records in non-provisioned populations: 23 plant species during 6 months (Lima and Ferrari, 2003), 68 plant species during 12 months (Stone, 2007), and 23 plant species during 8 months (Pinheiro et al., 2013). This suggests that our feeding data for squirrel monkeys was sufficient to cover the potential food fruit species. Nevertheless, sakis had a broader fruit repertoire. This evidence, combined with the fact that the two species consumed roughly the same amount of provisioned foods (interspecific comparisons were conducted only on wild fruits) indicates that the results of this study were not significantly affected by the availability of provisioned foods.

Advantages of eating fruits earlier

Sakis exhibited a prolonged use of shared wild fruit species compared to squirrel monkeys (Figure 5, Table S2). This factor contributed significantly to the higher proportion of wild fruit trees available for sakis throughout the study period compared to squirrel monkeys (Figure 6b). For example, sakis used the fruits of *Pouteria caimito* (Sapotaceae) for seven months, three of which were spent consuming only unripe seeds (Table S2). In contrast, squirrel monkeys only used *P. caimito* for the three months that they provided ripe pulp (Table S2). Regarding the fruit of *Lindackeria paludosa* (Achariaceae), squirrel monkeys only ate the visible aril of ripe fruits, which naturally split open, which limited the duration of fruit use to two months. In contrast, sakis ate *L. paludosa* seeds throughout the year by opening the fruits before they dehisced. Depending on the volume of fruits available and the number of consumers, destroying unripe fruits by foraging for seeds sakis could directly impact the future availability of ripe fruit for squirrel monkeys.

Sakis are not only adapted to eating young seeds, they may also be adapted to consuming unripe pulp compared to other primate species. In addition to the fact that sakis ate some unripe pulp (Table 2, Figure 4), it is possible that some of the “ripe pulp” was less mature than that eaten by squirrel monkeys. For example, the most frequently eaten wild fruit item by sakis was the "ripe" pulp of *Attalea maripa*—a species that squirrel monkeys never ate at our study site. However, *A. maripa* was the most important fruit for squirrel monkeys at other sites (Boinski, 1999; Pinheiro et al., 2013; Stone, 2007). According to Stone (2006, 2007), squirrel monkeys eat *A. maripa* pulp when the fruits are mature enough to be removed from the tree or after the fruits fall to the ground. At our study site, the sakis spent a lot of time on the fruiting *A. maripa* trees and seemed to use all the fruit before they matured.

Norconk (2020) and Cunningham (2006) also reported that sakis used fruits (*Pradosia caracasana* and *Licania discolor*) at several developmental stages (young seeds, mature pulp, and old seeds). Therefore, the fruit feeding system of sakis identifies aspects of a niche that is less restricted in the timing of fruit consumption. This generalized explanation provides a broader perspective on the ecology and evolution of pitheciines, going beyond their classification as mere seed eaters.

Importance of eating a diversity of fruit species

We hypothesized that the broader range of fruit species in the saki diet compared with squirrel monkeys would lead to a higher proportion of available fruit trees for sakis. To investigate this, we compared the number of fruit species used (Figure 3) and the proportion of available trees of non-shared fruit species between sakis and squirrel monkeys (Figure 6c). Contrary to our expectations, the difference in the number of fruit species used by sakis and squirrel monkeys did not significantly contribute to the higher proportion of fruit trees available to sakis compared to those available to squirrel monkeys (Figure 6c). This might be because the availability of shared fruit species was high at our study site. For example, fruits of the top three dominant species, *Euterpe oleracea*, *Siparuna guianensis*, and *Inga alba,* provided food for both primate species (Table 2 and Table S1). In addition, many fruit trees, such as *Mangifera indica* or *Inga edulis*, may have been planted or selectively grown for the benefit of humans, but are also commonly used by monkeys. For these reasons, at our study site, sakis eating shared fruits in an earlier developmental stage had a more significant effect on differentiating species diets than that of the fruit diversity. It remains possible that having access to a broader variety of fruit species could yield significant advantages in other environments with different compositions of plant species.

It is important to note that the fruit choice can be affected by various ecological and social factors. The body mass of squirrel monkeys (< 1 kg) is about half of that of sakis and, as is typical for primates of such a small size, insects make up a large proportion of their diet (Zimbler-DeLorenzo & Stone, 2011). The group size of squirrel monkeys was much larger, and more dispersed during foraging, than that of sakis. Future studies should consider how these factors affect foraging behavior between seed- and non-seed-eating primates, especially when comparing interspecific comparisons of multiple middle-sized frugivorous primates, to elucidate the uniqueness of the pitheciine feeding system.

Conclusion

In this study, we demonstrated that wild fruit availability was higher and more temporally stable for golden-faced sakis than for common squirrel monkeys: sakis had a longer consumption period for each fruit species than squirrel monkeys. Sakis used shared wild fruit species earlier and for longer periods than squirrel monkeys by using the fruits both at unripe and ripe stages. Thus, the saki fruit feeding system allows them to exploit a wider breadth of fruit species and extend the timing of fruit consumption, which seems to lead to a relative advantage in fruit availability compared with other sympatric primates.

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Tables

Table 1. Average daily diet composition of wild foods only in golden-faced sakis and common squirrel monkeys. Provisioned foods were excluded from calculations.

		Saki Group A (N = 40 d)	Saki Group B (N = 38 d)	Common squirrel monkey (N = 38 d)
Fruit	Pulp	28.3 ± 14.4%[†]	36.8 ± 15.4%	36.7 ± 15.6%
	Seeds	45.5 ± 18.4%	34.6 ± 15.1%	3.0 ± 6.4%
	Unknown part of fruits	6.9 ± 5.9%	9.7 ± 10.1%	1.5 ± 2.2%
Non-fruit	Flowers	3.1 ± 2.7%	1.8 ± 3.0%	8.0 ± 8.6%
	Leaves	10.6 ± 9.3%	11.0 ± 7.7%	0.09 ± 0.6%
	Insects	0.0	0.0	46.8 ± 13.1%
	Others	5.7 ± 4.5%	6.1 ± 5.1%	3.9 ± 5.9%

[†]Mean ± SD per day.

Table 2. List of fruit species used by the two primate species (Arranged by the number of feeding records in sakis).

Plant species	Family	Number of monitored trees†	Number of feeding records per fruit		Eaten part and ripeness‡	
			saki	squirrel monkey	saki	squirrel monkey
Attalea maripa	Arecaceae	17	486	0	Rp (486)	
Oenocarpus bacaba	Arecaceae	17	310	0	Rp (309), Ruk (1)	
***Lindackeria paludosa*§**	**Achariaceae**	**15**	**296**	**3**	**Us (171), Rs (111), UKs (11), UKuk (3)**	**Rp (3)**
Pouteria macrophylla	**Sapotaceae**	**25**	**217**	**1**	**Us (178), Rp (10), Rs(10), Ruk (8), UKs (5), Up (5), Uuk (1)**	**Rp (1)**
Siparuna guianensis	**Siparunaceae**	**40**	**197**	**90**	**Rs (142), Us (47), UKuk (6), UKs(2)**	**Rs (80), Rp (4), UKuk (3), Ruk (2)**
Inga edulis	**Fabaceae**	**3**	**180**	**85**	**Rp (70), Us (64), Uuk (21), Rs(16), Ruk (8), UKuk (1)**	**Rp(85)**
Pourouma guianensis	**Urticaceae**	**14**	**149**	**56**	**Rs (88), Us (34), Ruk (16), Rp (7), UKuk (3), UKs (1)**	**Rp (56)**
Protium spruceanum	Burseraceae	1	128	0	UKs (55), Us (37), Ruk (34), UKuk (2)	
Hevea brasiliensis	Euphorbiaceae	9	125	0	Rs (125)	
Pouteria caimito	**Sapotaceae**	**4**	**83**	**75**	**Rp (34), Us (27), Ruk (10), Rs (9), UKuk (2), Uuk (1)**	**Rp (75)**

Inga heterophylla	**Fabaceae**	**3**	**82**	**65**	**Rp (48), Us (20), UKuk (8), Ruk (3), UKp (1), Rs (1)**	**Rp(65)**
Arrabidaea prancei	Bignoniaceae		68	0	Us(62), UKs (6)	
Pseudima frutescens	Sapindaceae		66	0	Up (58), Rp (7), UKuk (1)	
Perebea mollis	**Moraceae**		**56**	**3**	**Us (48), Rs (5), UKs (2), UKuk (1)**	**Rp (3)**
Deguelia amazonica	Fabaceae		56	0	Us (47), Rs (9)	
Mangifera indica	**Anacardiaceae**	**1**	**55**	**75**	**Rp (52), UKp (2), Up (1)**	**Rp (75)**
Helicostylis tomentosa	**Moraceae**	**16**	**55**	**3**	**Us (20), Ruk (17), Rp (11), Rs (4), Uuk (1), UKs (1), UKuk (1)**	**Rp (3)**
Aparisthmium cordatum	Euphorbiaceae	4	53	0	Us (52), Rs (1)	
Lecythis lurida	**Lecythidaceae**	**1**	**51**	**1**	**Rs (28), Us (12), Ruk (10), Rp (1)**	**Rp (1)**
Protium apiculatum	Burseraceae		49	0	Ruk (45), Rp (3), UKuk (1)	
Simarouba amara	Simaroubaceae	1	49	0	Us (49)	
Ocotea grandifolia	**Lauraceae**		**46**	**1**	**Us (46)**	**Rp (1)**
Talisia macrophylla	Sapindaceae	4	43	0	Us (41), Rs (2)	
Ficus maxima	**Moraceae**	**13**	**42**	**9**	**UKp (30), UKuk (8), Uuk (3), Rpulp (1)**	**Ruk (6), UKp (3)**
Vouarana guianensis	**Sapindaceae**	**5**	**41**	**8**	**Rp (30), Us (5), Uuk (4), Up (1), UKuk (1)**	**Rp (8)**
Alchornea discolor	Euphorbiaceae		34	0	Us (23), Rs (11)	
Guarea silvatica	Meliaceae	2	33	0	Us (22), Rp (7), Rs (4)	
Virola polyneura	**Myristicaceae**		**32**	**4**	**Rp (32)**	**Rp (4)**

Bellucia grossularioides	**Melastomataceae**		**32**	**2**	**Rp(31), Up (1)**	**Rp (2)**
Inga alba	**Fabaceae**	**19**	**31**	**171**	**Rp (17), Ruk (6), Us (6), UKuk (2)**	**Rp (171)**
Pogonophora schomburgkiana	Peraceae	14	31	0	Us (26), Uuk (5)	
Brosimum guianense	Moraceae	8	29	0	Us (26), Uuk (2), Rp (1)	
Matayba arborescens	Sapindaceae	7	27	0	Rp (19), Up (6), Uuk (2)	
Syzygium cumini	**Myrtaceae**	**3**	**26**	**52**	**Rp (26)**	**Rp (52)**
Paullinia rugosa	**Sapindaceae**		**26**	**1**	**Rp (20), Ruk (3), Us (3)**	**Rp (1)**
Lacunaria jenmanii	Quiinaceae		26	0	Rp (12), Us (8), Ruk (5), Rs (1)	
Coccoloba parimensis	**Polygonaceae**		**25**	**25**	**Rp(25)**	**Rp (25)**
Bocoa viridiflora	**Fabaceae**	**8**	**23**	**2**	**Up (13), Us (9), Ruk (1)**	**Ruk (2)**
Passiflora sp.	Passifloraceae		23	0	Us (9), Rp (7), Rs (2), Uuk (2), Ruk (1), UKs (1), UKuk (1)	
Myrcia fallax	**Myrtaceae**	**15**	**22**	**34**	**Us (17), UKuk (4), Rp (1)**	**Rp (31), UKuk (3)**
Guarea sp.	Meliaceae		22	0	Rp (11), UKuk (7), Up (2), UKp (2)	
Unknown species 1			19	0	Us (11), UKs (8)	
Annona mucosa	**Annonaceae**	**3**	**17**	**110**	**Rp (12), Up (4), UKp (1)**	**Rp (110)**
Trichilia micrantha	Meliaceae		17	0	Us (9), UKuk (8)	
Casearia javitensis	**Salicaceae**		**16**	**1**	**Rp (8), Ruk (8)**	**Rp (1)**
Clitoria racemosa	Fabaceae	10	15	0	Us (14), Rs (1)	
Mabea caudata	Euphorbiaceae	1	15	0	Us (13), Rs (2)	
Trymatococcus amazonicus	Moraceae	3	14	0	Us (13), Rs (1)	

Unknown species 2			14	0	Us(14)	
Sorocea guilleminiana	**Moraceae**		**13**	**5**	**Rp (13)**	**Rp (5)**
Compsoneura ulei	Myristicaceae		13	0	Rs (6), Us (4), Rp (1)	
Dichapetalum rugosum	Dichapetalaceae		13	0	Rp (7), UKp (2), UKuk (2), Ruk (1), Up (1)	
Ocotea ujumari	Lauraceae	10	12	0	Us (12)	
Pouteria sp.	Sapotaceae		12	0	Rp (12)	
Unknown species 3			12	0	Us (12)	
Simarouba sp.	Simaroubaceae		12	0	Us (12)	
Lacmellea arborescens	**Apocynaceae**	**4**	**11**	**2**	**Uuk (7), UKp (3), Rp (1)**	**Rp (2)**
Inga sp.1	Fabaceae		11	0	Uuk (11)	
Pouteria cladantha	Sapotaceae		11	0	Rp (10), Ruk (1)	
Sorocea muriculata	Moraceae	1	11	0	Us (11)	
Eugenia patrisii	**Myrtaceae**	**3**	**10**	**5**	**Us (8), Rp (1), Ruk (1)**	**Rp(5)**
Cynometra bauhiniifolia	Fabaceae		10	0	Us (10)	
Lecythis prancei	Lecythidaceae	7	10	0	Us(10), Rs (1)	
Licania macrophylla	Chrysobalanaceae		10	0	Us (10)	
Socratea exorrhiza	Arecaceae		10	0	Rp (10)	
Unknown species 4			9	0	UKs (6), UKuk (3)	
Couepia ulei	Chrysobalanaceae		8	0	Rp (7), Us (1)	
Ipomoea mauritiana	Convolvulaceae		8	0	Rs (4), Us (2), UKuk (2)	
Swartzia tomentifera	Fabaceae		8	0	UKuk (4), Uuk (4)	
Inga sp.2	Fabaceae		8	0	Rp (7), Rs (1)	
Matayba oligandra	**Sapindaceae**		**7**	**3**	**Rp (6), UKp (1)**	**Rp (3)**
Inga obtusata	Fabaceae		7	0	Us (7)	
Lecythis pisonis	Lecythidaceae		7	0	Rs (3), Ruk (3), Rp(1)	
Eugenia punicifolia	**Myrtaceae**		**6**	**19**	**Rp (5), Uuk (1)**	**Rp (19)**

Anemopaegma oligoneuron	Bignoniaceae		6	0	Us (6)	
Xylopia sericea	Annonaceae	2	6	0	Us (4), UKs (2)	
Talisia esculenta	**Sapindaceae**	**2**	**5**	**132**	**Rp (5)**	**Rp (132)**
Leonia cymosa	**Violaceae**	**6**	**5**	**17**	**Rp (4), Up (1)**	**Rp(17)**
Euterpe oleracea	**Arecaceae**	**222**	**5**	**11**	**Up(3), Rp (2)**	**Rp (11)**
Anacardium occidentale	**Anacardiaceae**	**1**	**5**	**1**	**Rp (4), Us (1)**	**Rp (1)**
Strychnos amazonica	Loganiaceae		5	0	UKuk (3), Us (2)	
Unknown species 5			5	0	UKp (5)	
Inga umbratica	**Fabaceae**	**1**	**4**	**1**	**Rp (4)**	**Rp (1)**
Syzygium malaccense	**Myrtaceae**		**4**	**1**	**Rp (3), Up (1)**	**Rp (1)**
Garcinia madruno	Clusiaceae	2	4	0	Rp (2), Up (2)	
Guatteria scytopylla	Annonaceae	25	4	0	Rp (4)	
Paypayrola grandiflora	Violaceae		4	0	Us (4)	
Schefflera morototoni	Araliaceae	6	4	0	UKs (3), UKuk (1)	
Unknown species 6			4	0	UKs (4)	
Unknown species 7			4	0	Us (4)	
Unknown species 8			4	0	Us (4)	
Miconia regelii	**Melastomataceae**	**4**	**3**	**29**	**Rp (3)**	**UKp (15), Rp (14)**
Bocageopsis multiflora	**Annonaceae**	**6**	**3**	**6**	**Rp (3)**	**Rp (6)**
Casearia arborea	**Salicaceae**	**4**	**3**	**3**	**UKuk (3)**	**Ruk (3)**
Oenocarpus minor	**Arecaceae**		**3**	**2**	**Rp (3)**	**Rp (2)**
Tapirira guianensis	**Anacardiaceae**	**12**	**2**	**18**	**Uuk (2)**	**Rp (12), Up (5), UKp (1)**
Garcinia brasiliensis	**Clusiaceae**		**1**	**45**	**Rp (1)**	**Rp (45)**
Cordia bicolor	**Ehretiaceae**	**14**	**1**	**12**	**Rp (1)**	**Rp (12)**
Euterpe precatoria	**Arecaceae**	**10**	**1**	**3**	**Rp (1)**	**Rp (3)**
Cissus verticillata	Vitaceae		0	51		Rp (51)
Muntingia calabura	Muntingiaceae		0	27		UKp (12), Up (10), Rp (5)
Zanthoxylum rhoifolium	Rutaceae	3	0	27		Rs (17), UKs (6), Ruk (3)

Psidium guajava	Myrtaceae		0	26	Rp (26)
Psidium sp.	Myrtaceae		0	20	Rp (19), UKuk (1)
Spondias mombin	Anacardiaceae	11	0	20	Rp (20)
Musa sp.	Musaceae		0	17	Rp (16), Up (1)
Morus alba	Moraceae		0	15	Rp (14), UKuk (1)
Astrocaryum aculeatum	Arecaceae	8	0	9	Rp (8), UKp (1)
Inga lateriflora	Fabaceae		0	9	Rp (9)
Mezia includens	Malpighiaceae		0	9	Us (6), UKs (3)
Erythroxylum macrophyllum	Erythroxylaceae	6	0	8	Rp (8)
Unknown species 46			0	7	UKuk (7)
Unknown species 47			0	7	UKuk (7)
Inga melinonis	Fabaceae		0	6	Rp (6)
Unknown species 48			0	5	Rp
Carica papaya	Caricaceae	3	0	4	Rp (4)
Ocotea oblonga	Lauraceae		0	4	Rp (4)
Ocotea sp.1	Lauraceae		0	4	Ruk (4)
49 more non-shared species for saki[¶]			77	0	
15 more non-shared species for squirrel monkeys			0	27	
Total			3,973	1,494	

[†]Plant species with these numbers were included in the 1,000 trees/vines monitored in the fruit census and used for the calculation of species-specific fruit availability.

[‡]"U," "R," and "UK" represent unripe, ripe, and unknown ripeness, respectively; "s," "p," and "uk" represent seed, pulp, and unknown part, respectively. The numbers within parentheses represent the number of feeding records for each fruit item.

[§]43 species in **bold type** are shared fruit species (eaten by both primate species).

[¶]Plant species that were used less than four times by only one primate species were grouped together.

Figure legends

Figure 1. Campus I (circled by a dashed line) of the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Amazonas, Brazil (3°09´S, 59°99´W) (Map data: Google, Image© 2022 Maxar Technologies, Image© 2022 CNES/Airbus). The provisioning tables for monkeys are represented by white triangles (tables for cut bananas, papayas, and pineapples) and circles (tables for coconut flesh). Yellow horizontal lines represent the 16 fruit census transects.

Figure 2. Monthly changes in environmental factors at the study site from January 2019 to February 2020. a) Monthly precipitation and mean temperature. The data were obtained from the Banco de Dados Meteorológicos on the website of the Instituto Nacional de Meteorológia (INMET). b) Proportion of fruiting trees and vines recorded in the monthly fruit census, regardless of whether they were used by monkeys.

Figure 3. Rarefaction curves (solid lines) and extrapolation (dashed lines) of wild fruit species eaten by golden-faced sakis (*Pithecia chrysocephala*) and common squirrel monkeys (*Saimiri sciureus*). The 95% confidence intervals (shaded regions) were obtained by a bootstrap method with 100 replications.

Figure 4. Proportion of the eaten fruit part and developmental stage for the shared wild fruit species in golden-faced sakis (*P. chrysocephala*) and common squirrel monkeys (*S.*

sciureus). Only results of feeding records including both the developmental stage and the fruit part are shown (N = 1,656 records for sakis and N = 1,154 records for squirrel monkeys).

Figure 5. Number of months that each primate species used each shared fruit species. Each point represents a fruit species (N = 43).

Figure 6. Proportion of available fruiting trees and vines for golden-faced sakis (*P. chrysocephala*) and common squirrel monkeys (*S. sciureus*). We separately showed the a)total proportion,the proportion for b) shared fruit species, and c) Non-shared fruit species. . Comparison of availability of shared species in graph b) shows the differences caused by the different consumption periods for the same fruit species. Comparison of availability of non-shared fruit species in graph c) shows differences caused by using fruit species that are not used by the other primate species.