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Article

Fruit and Leaf Selection Based on Plant Species and Maturity in Black-Handed Spider Monkeys (*Ateles geoffroyi*)

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Simple summary: Primates select food items based on their physical and chemical properties which can vary depending on the plant species, plant part, and plant maturity. Although spider monkeys are known to feed primarily on ripe fruits, they also consume unripe fruits and other plant parts such as leaves. However, the specific selection patterns for fruits and leaves are still unknown. Therefore, we analyzed the physical and chemical properties of unripe and ripe fruits as well as young and mature leaves, from six plant species to assess their influence on spider monkeys' food selection. The spider monkeys exhibited different selection patterns for fruits and leaves, even though, in both cases, selection was primarily influenced by maturity and plant species. We conclude that spider monkeys are more selective when choosing fruits than when choosing leaves.

Abstract: Food selection in primates is guided by a sensory evaluation of the physical and chemical properties of the foods. These properties vary with plant species, plant part, and plant maturity. Spider monkeys generally consume ripe fruits, but their diet also includes unripe fruits and young and mature leaves from a wide variety of plant species. We evaluated food selection in ten adult black-handed spider monkeys (*Ateles geoffroyi*) living in a controlled environment in Catemaco (Veracruz, Mexico). We used six plant species which are part of their natural diet and compared selection between ripe and unripe fruits and young and mature leaves, respectively, for the same plant species. We also analyzed the sucrose content, pH, size, and color of fruits and the color and size of leaves of each plant species. For fruit selection, our model showed that 75% of choices depended on an association between the plant species and the stage of maturity. In contrast, our model predicted 52% of the leaf selection, and monkeys considered both the stage of maturity and the plant species. Our results suggest that *Ateles geoffroyi* exhibit a more specific food selection for fruits than leaves, resulting in different food choices based on the physical and chemical properties of these food items.

Keywords: food choice; physical and chemical properties; sucrose; frugivory; primate

1. Introduction

Primates have diverse diets, primarily consisting of plants (Lambert & Rothman, 2015; Richard, 1985). Plant parts vary in their chemical composition, like sugar content, pH, secondary metabolites and fiber content, and in external physical properties, like color, texture and size (Del Bubba et al., 2009). Primates evaluate the physical and chemical properties of food from handling to consumption (Dominy et al., 2001; Laska et al., 2000a, 2009; Sánchez Solano et al., 2022; Sclafani, 2001; Stroebel et al., 2004; Valenta et al., 2013, 2018a). When choosing a fruit, primates have been reported to use color, size, pH, and sugar content as sensory cues. For example, *Alouatta* spp. *Callithrix geoffroyi*, *Cebus apella*,

and *Hylobates* spp. choose yellow, orange, red, and brown fruit (Caine & Mundi, 2000; Dominy & Lucas, 2001; Regan et al., 2001). Other primates, like *Cercopithecus ascanius*, *Cercopithecus mitis* and *Colobus guereza*, select fruits from 1 cm to 7.5 cm in diameter (Flörchinger et al., 2010; McConkey et al., 2002). Several primate species select fruits with a pH ranging from 2 to 5 (Dominy et al., 2001; Laska et al., 2000a; Sánchez-Solano et al., 2022; Ungar, 1995), and those with high sugar content (Riba-Hernández et al., 2003; Stevenson, 2004; Ungar, 1995). Primates that consume leaves also use properties such as color and size as sensory cues for their food choices. For example, *Alouatta palliata* choose yellow, light green, or reddish colored leaves, and prefer small leaves (Melin et al., 2017; Sánchez-Solano et al., 2020).

The foods that primates select are usually beneficial for their nutritional balance and correspond to their sensory capacity and familiarity. Primates are more likely to consume other foods when preferred foods are unavailable in search of potential energy and nutritional gains (Huskisson et al., 2021) and might modulate their decision-making based on the physical and chemical properties of fruits and leaves.

The relatively controlled conditions of captivity provide an opportunity to evaluate the influence of the physical and chemical properties of foods and plant species on food selection. For example, captive *Alouatta guariba clamitans*, *Saimiri sciureus*, *Macaca nemestrina*, *Pithecia pithecia*, and *Ateles geoffroyi* select cultivated food non-opportunistically (Laska, 2001; Martins et al., 2023; Silveira et al., 2024). Cultivated foods have different physical and chemical properties compared to their wild counterparts, influencing the food selection of primates (Lambert & Rothman, 2015; Silveira et al., 2024).

Dietary specialist primates, like spider monkeys, select food based on high energy content while avoiding limiting compounds such as secondary metabolites and fiber using sensory cues offered by the physical and chemical properties of the different plant parts (Del Bubba et al., 2009; Riba-Hernández et al., 2003). Spider monkeys are mainly frugivorous, and wild spider monkeys dedicate 55-90% of their feeding time to ripe fruits (Di Fiore et al., 2008). However, they also consume unripe fruits, and other plant parts such as leaves, seeds, flowers and bark (Felton et al., 2008, 2009; González-Zamora et al., 2009). Leaves can represent as much as 37% of spider monkeys' feeding time (de Luna et al., 2017), and the percentage of total feeding time on young leaves is higher than (7.3%) on mature leaves (1.2%) (Chapman, 1987). This suggests that leaf maturity and the associated changes in macronutrient content may play a role in leaf choice (Felton et al., 2009). Captive black-handed spider monkeys have been reported to select fruits with high amounts of lipids and sugars (Laska et al., 2000b). However, corresponding data on possible correlations between the selection of leaves and their chemical composition are lacking for spider monkeys.

We aimed to assess food selection patterns of *Ateles geoffroyi* related to the stage of maturity of fruits and leaves from six plant species. We asked the following questions: 1) do the physical and chemical properties of fruits and leaves vary with maturity stage? and 2) how does the maturity of different fruits and leaves influence the food selection of *A. geoffroyi*? We hypothesized that *Ateles geoffroyi* are flexible in their food selection depending on the maturity stage of fruits and leaves. We predicted that *A. geoffroyi* uses different physical and chemical properties (sucrose, pH, color, and size) related to the maturity stage of both fruits and leaves.

2. Methods

2.1. Site and study subjects

We conducted our study at the "Hilda Avila de O'Farrill" Environmental Management Unit of the Universidad Veracruzana, near Catemaco in the Los Tuxtlas region (Veracruz, Mexico), from March to August 2022. We conducted tests on five adult female and five adult male spider monkeys. The subjects were kept in individual enclosures (4 m x 4 m x 4 m) connected by sliding doors that allowed them to interact but be separated for individual testing. All individuals were exposed to natural conditions of temperature, relative humidity and light-dark cycles. We did not deprive the monkeys of food but conducted all experiments 2 hours before feeding to ensure that they were motivated. We fed the monkeys a diet of cultivated fruits and vegetables, which varied with fruit availability and seasonality (avocado, banana, mango, tomato, apple, pear, orange, papaya, melon, prickly pear, pineapple, celery, beet, chard and broccoli).

2.2. Fruit and leaf collection

We collected unripe and ripe fruits, and young and mature leaves, from six plant species that are part of the diet of wild spider monkeys at Los Tuxtlas (González-Zamora et al., 2009): *Ficus colubrinae*, *Ficus rzedowskiana*, *Ficus yoponensis*, *Spondias mombin*, *Spondias radlkoferi* and *Poulsenia armata*.

We collected fresh food items on the morning of each test day. We selected trees with available fruits and leaves and collected samples from the middle layer, reported as more accessible to fruits and leaves (Feagle et al., 2024). We collected 50 samples of unripe fruit (UF), ripe fruit (RF), young leaf (YL) and mature leaf (ML), from each plant species, resulting in 100 fruits and 100 leaves for each species/day for 5 days. We estimated the maturity stage of fruits and leaves based on color, size and consistency (Di Fiore et al., 2008; Felton et al., 2008; 2009). Additionally, we collected, depending on their availability, a range of 17-28 fruits and 17-28 leaves from each maturity stage to measure fruit sucrose content, pH, color, and size, and leaf color and size.

2.3. Selection tests

We presented food items to the animals on the same day that we collected them. We conducted one session per day for fruits and one for leaves for five consecutive days for each plant species. In each test we simultaneously presented five items from each maturity stage of the same plant species pseudo-randomly on a 50 cm x 30 cm metal tray. We presented the tray to the monkeys 20 cm away from the mesh of the enclosure and allowed them to take and consume food items for 1 min. We recorded the number of ripe and unripe fruits and young and mature leaves consumed from each plant species.

2.4. Analysis of the physical and chemical properties of the fruits and leaves

We measured sucrose content, pH, color and size in unripe and ripe fruits and color and size in young and mature leaves. We measured the sucrose concentration by placing a drop of fruit juice in a refractometer (Atago® Automatic Brix 0.0 ~ 33.0%; Kitamura et al., 2004; Pablo-Rodríguez et al., 2015; Sánchez-Solano et al., 2022). We measured the pH by placing a drop of fruit juice on a test strip (HICARER®). We photographed each item with a moto G9 plus cell phone with a main sensor rear camera: 64 MP (1/1.73"), f/1.8, PDAF, ultra-angular: 8 Mega Pixels (MP) (1/4.0"), f/2.2, Depth 2 MP f/2.2 and Macro: 2 MP f/2.2. We took all photographs using a white LED light ring (NOVOLUNE®). We measured color (RGB composition) and size by analyzing photographs (Chen et al., 2020; Yadav et al., 2010) with the program ImageJ (v 1.52a).

2.5. Statistical analysis

We used ANOVAs to compare the physical and chemical properties between unripe and ripe fruits (sucrose, pH, color and size as dependent variables) and between young and mature leaves (color and size as dependent variables) of the different plant species. When the ANOVA was significant, we used TukeyHSD *post hoc* tests to determine which physical and chemical properties showed significant differences in maturity stage (Hothorn et al., 2008; Kassambara, 2023). We used the partial η^2 as the size effect calculated with the library effect size (Ben-Shachar et al., 2020).

We used models to test our predictions regarding how *A. Geoffroyi* considers different physical and chemical properties that are associated with the maturity stage of various species of fruits and leaves, respectively. We used generalized linear mixed models, using the number of selected ripe and unripe fruits or mature and young leaves as the dependent variables, to model selection of ripe and unripe fruits and young and mature leaves, respectively, from the same plant species. We ran five models for fruit selection and five models for leaf selection with increasing numbers of fixed effects and interactions. Model 1 included only the random effect individual identity (1 Individual). We included this random effect in all subsequent models. Model 2A evaluated maturity stage as a fixed effect (State + (1 Individual)). Model 2B evaluated only the plant species as a fixed effect (Species + (1 Individual)). Model 3 considered maturity stage and plant species together as fixed effects (State + Species + (1 Individual)). Model 4 evaluated maturity stage nested within species (State/Species + (1 Individual)). We fitted models with Poisson distribution and a log-link function. We report the Akaike Information Criterion (AIC), the r^2 of the random effects, and the r^2 of the fixed effects for each model.

We conducted all analyses using R (R Core Team, 2023). We used the lme4 library and the glmer function (Bates et al., 2015) to fit the models. We used the rsq library (Zhang, 2023) to calculate the r^2 values for each model.

3. Results

3.1. Physical and chemical characterization of food items

Fruit sucrose content, pH, and size varied significantly among plant species, between ripening stages, and according to the interaction of these two variables (species and ripening stage) (Table 1). We also found significant differences between plant species, ripening stages, and interaction of these two variables on red and blue colors. For green, we found significant effects for plant species and the interaction term, but not for ripening stage (Table 1). Sucrose concentration was significantly higher in ripe fruits than in unripe fruits across all six species, and the pH was less acidic in the ripe fruits except for *Spondias mombin* (Figure 1). The RGB color composition of fruits varied: three of the six species turned reddish when mature, the green color decreased in two species, and the blue color increased in only two species (Figure 1). Ripe fruits were significantly larger than unripe fruits in four species, while we found no significant differences in the size of fruits of *Spondias mombin* and *Spondias radlkoferi* as a function of ripeness.

Table 1. Results of ANOVA of the physical and chemical properties of fruits consumed by spider monkeys in Los Tuxtlas region, Veracruz, Mexico, from March to August 2022.

Fruit physical-chemical characteristics	Variable	F	p	Partial η^2
Sucrose	Species	(5, 237) = 68.18	<0.001	0.20
	Ripe state	(1, 237) = 1002.34	<0.001	0.58
	Interaction	(5, 237) = 30.54	<0.001	0.09
pH	Species	(5, 237) = 151.81	<0.001	0.46
	Ripe state	(1, 237) = 206.20	<0.001	0.13
	Interaction	(5, 237) = 86.38	<0.001	0.26
Red	Species	(5, 237) = 46.68	<0.001	0.16
	Ripe state	(1, 237) = 563.43	<0.001	0.37
	Interaction	(5, 237) = 94.18	<0.001	0.31
Green	Species	(5, 237) = 59.275	<0.001	0.30
	Ripe state	(1, 237) = .087	0.768	<0.001
	Interaction	(5, 237) = 92.553	<0.001	0.46
Blue	Species	(5, 237) = 20.19	<0.001	0.20
	Ripe state	(1, 237) = 66.28	<0.001	0.13
	Interaction	(5, 237) = 22.23	<0.001	0.22
Size	Species	(5, 237) = 544.69	<0.001	0.81
	Ripe state	(1, 237) = 255.20	<0.001	0.08
	Interaction	(5, 237) = 30.08	<0.001	0.04

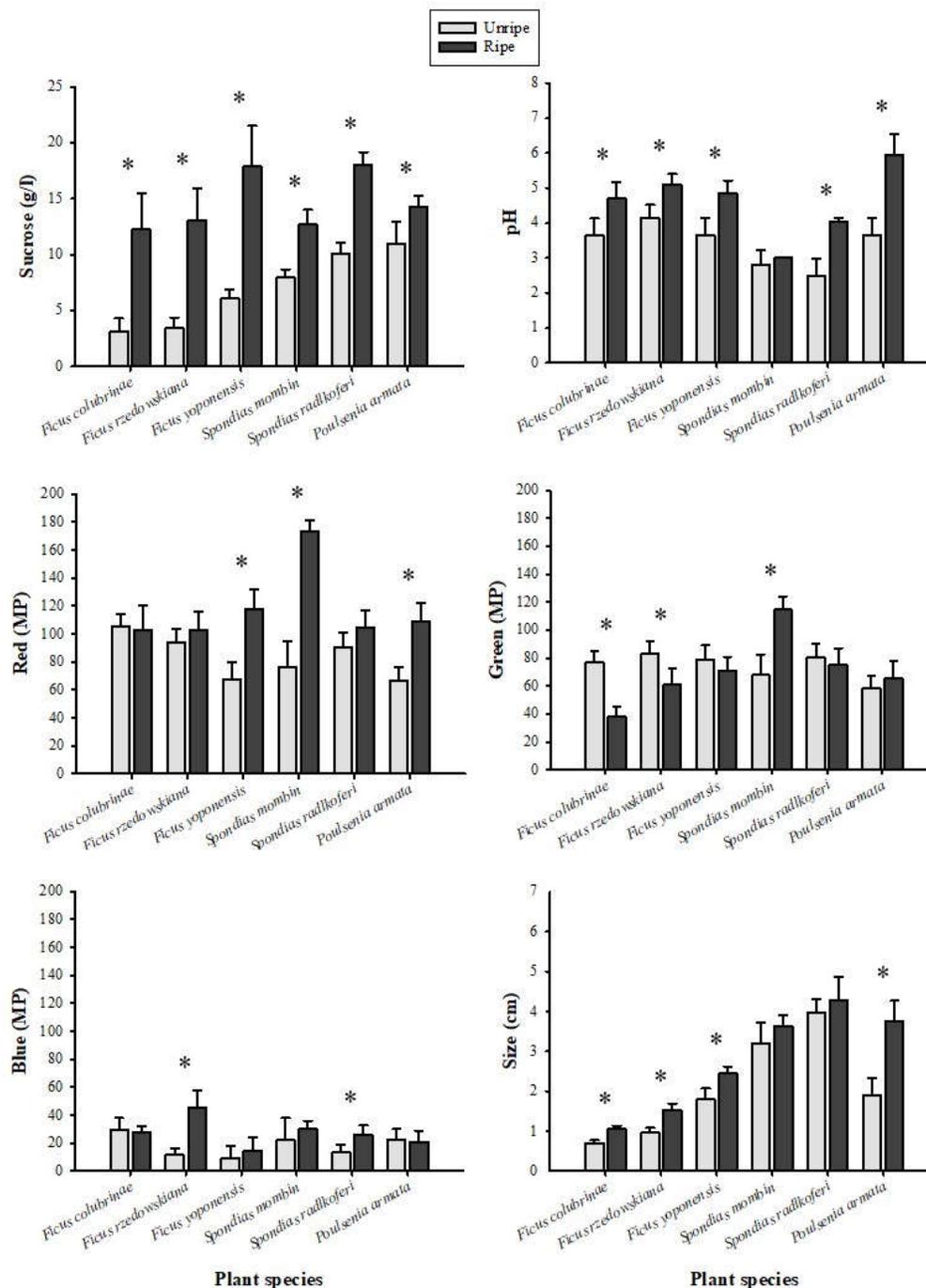


Figure 1. Physical and chemical properties of fruits (mean \pm SD) consumed by spider monkeys in Los Tuxtlas region, Veracruz, Mexico, from March to August 2022. (*) Indicates significant Tukey HSD tests ($p < 0.01$).

For the leaves we found significant effects of the plant species, maturity stage, and the interaction of these two variables on green and blue color. In the case of red color, the interaction had a significant impact, but not the maturity stage (Table 2). We found significant effects of the interaction between plant species and ripening state on leaf size (Table 2). The post hoc Tukey HSD tests revealed significant differences in RGB color intensity, with green exhibiting higher intensity than red and blue (Figure 2). Mature leaves were significantly larger than young leaves in three of the six plant species (Figure 2).

Table 2. ANOVAs of the physical and chemical properties of leaves consumed by spider monkeys in Los Tuxtlas region, Veracruz, Mexico, from March to August 2022.

Leaves physical-chemical characteristics	Variables	F	p	Partial η^2
Red	Species	(5, 228) = 13.420	<0.001	0.13
	Mature state	(1, 228) = 1.667	0.198	0.003
	Interaction	(5, 228) = 40.194	<0.001	0.40
Green	Species	(5, 228) = 6.638	<0.001	0.09
	Mature state	(1, 228) = 10.147	0.001	0.03
	Interaction	(5, 228) = 17.911	<0.001	0.25
Blue	Species	(5, 228) = 49.38	<0.001	0.31
	Mature state	(1, 228) = 148.32	<0.001	0.18
	Interaction	(5, 228) = 36.26	<0.001	0.23
Size	Species	(5, 228) = 88.989	<0.001	0.60
	Mature state	(1, 228) = 46.545	<0.001	0.06
	Interaction	(5, 228) = 4.295	<0.001	0.03

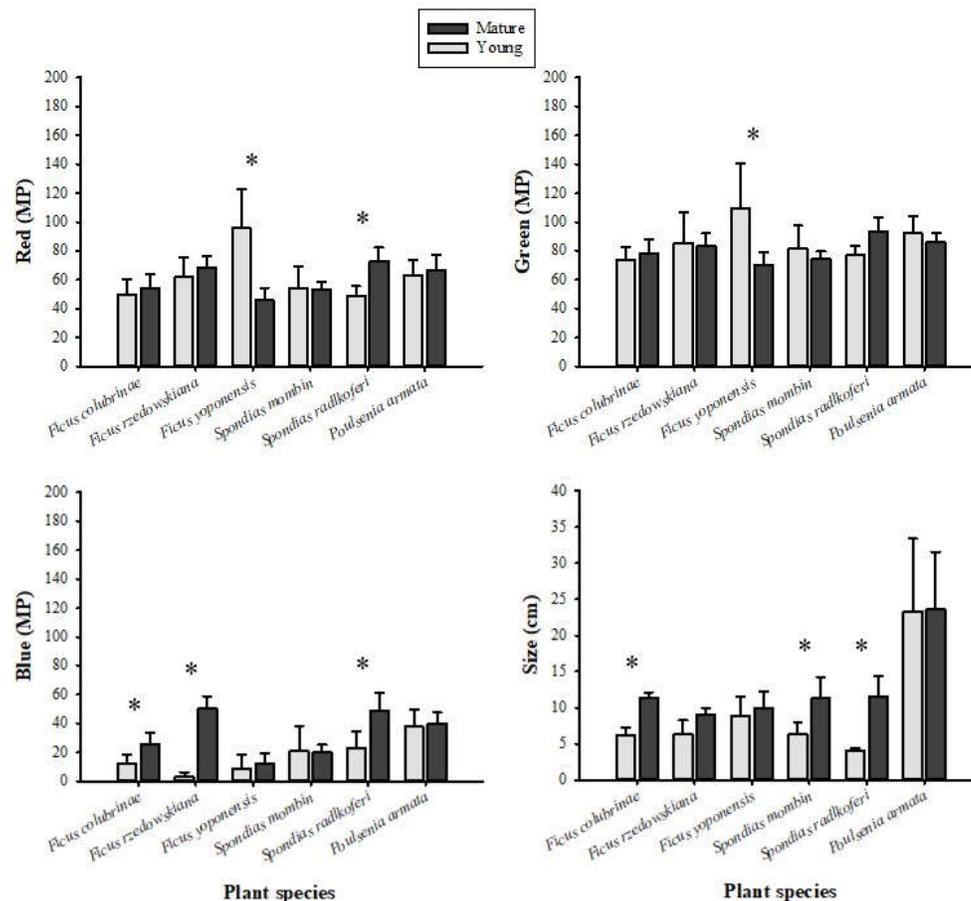


Figure 2. Physical and chemical properties of leaves (mean \pm SD) consumed by spider monkeys in Los Tuxtlas region, Veracruz, Mexico, from March to August 2022. (*) Indicates significant Tukey HSD tests ($p < 0.01$).

3.2. Food selection

All individuals selected more ripe fruits than unripe fruits (Figure 3). Once ripe fruits were no longer available, the monkeys selected unripe fruits of all species except for *Poulsonia armata*, of which no unripe fruit was consumed (Figure 3). From our GLMMs, Model 4 showed the lowest AIC values

with a decrease of more than 100 units and an increase in the r^2 of the full model compared with Model 3 (Table 3). The GLMMs showed that individual variability (r^2 random) accounted for approximately 5% of data in Model 4 (Table 3).

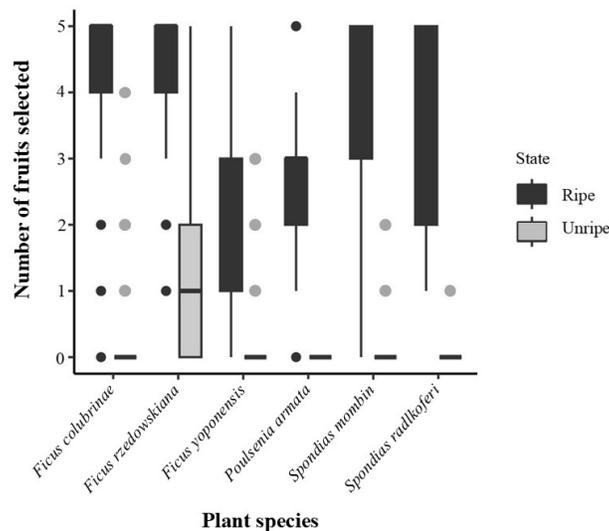


Figure 3. Number of unripe and ripe fruits selected from six plant species by spider monkeys in Catemaco, Veracruz, Mexico, from March to August 2022. Ripe fruits are represented in black, while unripe fruits are represented in grey. Plots represent the monkey's selection of fruits (mean \pm SD).

Table 3. Results of the models for fruits collected in Los Tuxtlas region, Veracruz, Mexico, from March to August 2022.

Model	AIC	r^2 fixed effects	r^2 random	r^2 full model
1. Individual	2495.6	-	0.029	0.029
2A. State + (1 Individual)	1699.9	0.566	0.045	0.611
2B. Species + (1 Individual)	2388.4	0.033	0.091	0.12
3. State + Species + (1 Individual)	1592.7	0.65	0.042	0.692
4. State/Species + (1 Individual)	1484.9	0.694	0.051	0.746

Spider monkeys selected more young than mature leaves. They consumed young leaves from all species, and mature leaves from all species except *Poulsonia armata* (Figure 4). In the GLMMs, Model 4 (fixed nested effects) had the lowest AIC values and the greatest r^2 for the full model. However, the reduction of the AIC between Model 3 and Model 4 was smaller than the reduction between Model 3 and Models 2A and 2B (Table 4). The r^2 for the full model was similar in Models 3 and 4. Based on parsimony (simple fixed effects relations instead of nested interactions), we chose Model 3 to describe leaf selection. Model 3 showed that individual variability (r^2 random) accounted for 10% of the data for leaves (Table 4).

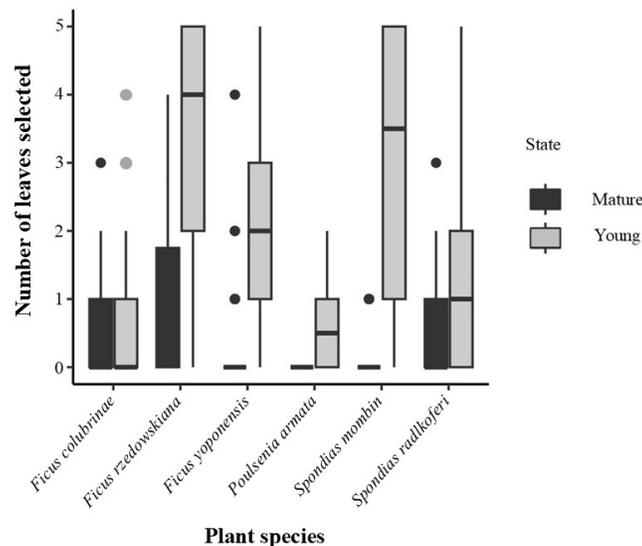


Figure 4. Number of young and mature leaves selected from six plant species reported in the diet of spider monkeys in Catemaco, Veracruz, Mexico, from March to August 2022. Mature leaves are represented in black, while young ones are represented in grey. Plots represent the monkey's selection of leaves (mean + SD).

Table 4. Results of the models for leaves collected in Los Tuxtlas region, Veracruz, Mexico, from March to August 2022.

Model	AIC	r^2 fixed effects	r^2 random	r^2 full model
1. Individual	1881.8	-	0.073	0.073
2A. State + (1 Individual)	1587.5	0.214	0.099	0.314
2B. Species + (1 Individual)	1706.5	0.132	0.074	0.207
3. State + Species + (1 Individual)	1412.2	0.418	0.101	0.519
4. State/Species + (1 Individual)	1355.4	0.438	0.107	0.546

4. Discussion

We found significant differences in the physical and chemical properties of unripe and ripe fruits from the same plant species. Sucrose levels increased in all species during ripening. The acidity of five of the six fruit species decreased once they reached ripeness. Color intensity changed differently across the fruit species: three increased in red, two decreased in green, and two increased in blue. The size of the fruit also increased significantly with ripening in four of the six species. The physical and chemical properties of the fruits from the six plant species we examined fell within the ranges reported for fruits consumed by other primate species (Dominy et al., 2001). We also found that leaves changed in color and size with maturity. The intensity of the blue color (in three of the six plant species) increased in mature leaves compared to young leaves, and mature leaves were larger than young leaves in three of the six plant species.

The concentration of sucrose in the fruits we analyzed here was higher than the gustatory thresholds for sucrose in *Ateles geoffroyi* (Laska et al., 1996) and is consistent with the sucrose concentrations found in fruits chosen by *A. geoffroyi* in the wild (Pablo-Rodríguez et al., 2015). Our finding that spider monkeys preferred ripe over unripe fruits supports the notion that the concentration of sucrose in ripe fruits may play a role in fruit selection. The acidity of fruits consumed by the spider monkeys in our study was also similar to the pH reported for fruits consumed by other primates (Dominy et al., 2001; Laska et al., 2000a; Ungar, 1995). The concentration of sucrose and acidity in fruits is likely to serve as a criterion to assess the ripeness, as suggested for *Pongo pygmaeus*, *Macaca fascicularis*, *Hylobates lar* including *Ateles geoffroyi* (Dominy et al., 2001; Laska et al., 2000a).

The intensity of red or blue color associated with maturity is thought to be a visual cue aiding the selection of mature fruits in some primate species, particularly those with trichromatic vision (Lomáscolo & Schaefer, 2010; Valenta et al., 2018b). The fruits we analyzed here changed color during maturation. In some cases, they increased in red and blue tones when ripe, and in some cases, they decreased in greens. *Ateles geoffroyi* has polymorphic vision, with males being dichromats while females may be trichromats or dichromats (Veilleux et al., 2021). However, dichromats may not be less efficient in fruit selection as vision plays only a limited role in food selection, with other senses also involved, as reported in frugivorous primates (Melin et al., 2009; 2014; Valenta et al., 2018b). We found that ripe fruits were larger than unripe fruits, which fits to the notion that size may also serve as a visual cue for fruit selection by spider monkeys, as described for other frugivorous primates (Flörchinger et al., 2010; McConkey et al., 2002).

We found that mature leaves were larger than young leaves in some plant species consumed by spider monkeys in the wild, but not in *Ficus rzedowskiana*, *Ficus yoponensis*, and *Poulsenia armata*. Young leaves of *F. rzedowskiana*, *F. yoponensis*, *S. mombin*, and *P. armata* were greener than mature leaves, but *F. colubrinae* and *S. radlkoferi* leaves showed the opposite pattern. Our results suggest that primate species with polymorphic color vision, such as *A. geoffroyi*, select young leaves based on both size and their red hues (Lucas et al., 1998; Melin et al., 2017). Primates have repeatedly been reported to use changes in leaf color and size to evaluate maturity stage, and, in some cases those characteristics are related to protein contents, toughness, and secondary metabolites (Veilleux et al., 2022).

We found that 75% of fruit selection by *Ateles geoffroyi* was influenced by fruit maturity (State/Species + (1 Individual)). This finding suggests that most of the fruits of the plant species we studied undergo similar changes in sucrose content and pH, making them more attractive when ripe (Dominy et al., 2001; Laska et al., 2000a; Lomáscolo & Schaefer, 2010; Riba-Hernández et al., 2003, 2005; Stevenson, 2004; Ungar, 1995; Valenta et al., 2018b). However, differences in chemical properties such as sucrose content and pH levels may affect the palatability of plants. It has been proposed that *A. geoffroyi* selects fruits using the ratio between sweetness and sourness as a criterion (Laska et al., 2000a; Pablo-Rodríguez et al., 2015). Our findings support the idea that gustatory cues may play a role in fruit selection (Laska et al., 2000b).

We found that *A. geoffroyi* consistently preferred ripe fruits but also ate some unripe fruits from five of the six species tested. This is in line with findings from previous studies showing that *Ateles* spp. prefer ripe over unripe fruit (Di Fiore et al., 2008). However, when ripe fruits were no longer available, the spider monkeys also consumed unripe fruit. Thus, our results support the notion that these primates are flexible in their food choices depending on availability of preferred items (Laska et al., 2000b). In our study, *A. geoffroyi* avoided the unripe fruits of *Poulsenia armata*, although the sucrose levels, pH, size, and color of this fruit species were within the range of the other unripe fruits consumed. Besides the ratio between sweetness and sourness, color, and size, other chemical properties such as the content of plant secondary metabolites or fiber that we did not measure in our study may influence food selection and thus explain the avoidance of some plants.

We found that the maturity stage influenced 52% of spider monkeys' leaf selection (State + Species + (1 Individual)). This finding is consistent with those of previous studies in spider monkeys which showed a higher consumption of young than mature leaves (Felton et al., 2008, 2009; González-Zamora et al., 2009). However, other factors may also influence leaf selection. For example, fiber content and plant secondary metabolites can vary depending on ultraviolet radiation, water stress, pathogens, and plant defense strategies against herbivores (Akula & Ravishankar, 2011; de Andrade et al., 2021; War et al., 2012; Yang et al., 2018). Fiber and plant secondary metabolites have been reported to affect the selection of leaves and the assimilation of nutrients in primates such as *Pongo pygmaeus*, *Pongo abelii*, *Presbytis entellus*, *Alouatta guariba* and *Alouatta palliata* (Glander, 1978; Kar-Gupta & Kumar, 1994; Leighton, 1993; de Andrade et al., 2021; Schmidt et al., 2005; War et al., 2012; Windley et al., 2022). Spider monkeys may also use fiber content and the content of plant secondary metabolites to select leaves. There are reports that *Ateles hybridus* increases leaf consumption when fruits are scarce (De Luna et al., 2017), suggesting that for spider monkeys the assessment of the physical and chemical properties of leaves are important when fruits are scarce.

We also found individual differences in fruit and leaf selection by *A. geoffroyi*, depending on the plant part. Individual variation accounted for 5% of variation in fruit selection, and 10% of variation in leaf selection. Individual variability has also reported in the selection of cultivated fruits by spider

monkeys (Laska et al., 2000b). Species like *Ateles belzebuth belzebuth* and *Ateles chamek* prefer ripe fruits (Suarez, 2006; Wallace, 2005), and are thought to be more selective for fruits than for leaves (Figure 5). Spider monkeys are considered as ripe-fruit specialists, and have been reported to select food items high in metabolizable energy. However, they can consume other, nutritionally less favorable food items (like leaves, flowers, bark, and roots) when their preferred foods are unavailable (Huskisson et al., 2021; Lakshminarayanan et al., 2011). This flexibility has also been reported in primates like *Pan troglodytes*, *Gorilla gorilla gorilla* and *Macaca fuscata*, that consume a variety of fruits, leaves, and other plant parts (Huskisson et al., 2021; Lakshminarayanan et al., 2011). Such dietary flexibility may be supported by physiological adaptations, such as changes in saliva composition that occur in response to an increase in plant secondary metabolites like tannins (Ramírez-Torres et al., 2022).

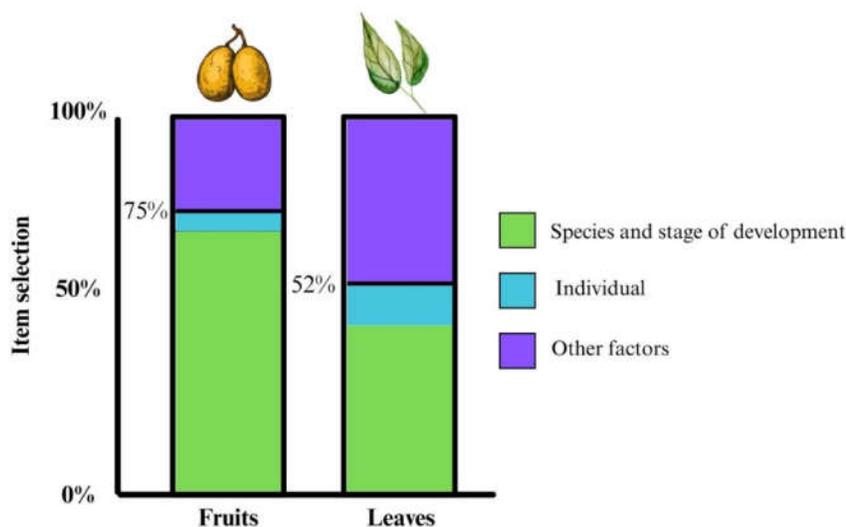


Figure 5. Proposed model of the factors involved in fruit and leaf selection in *Ateles Geoffroyi*.

5. Conclusion

Food selection in *Ateles Geoffroyi* is influenced by the plant species and the developmental stage of food items, especially in fruits. Individual preferences also influence food selection. Future studies should consider other physical and chemical properties of food items, such as odors, texture and hardness, that may shape food selection.

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Institutional Review Board Statement: The experiments reported here comply with the Guidelines for the care and use of mammals in neuroscience and behavioral research (National Research Council, 2011) and with the Mexican law (NOM-062-ZOO-1999 and NOM-051-ZOO-1995). The research protocol was approved by the board of ethics of the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT [SGPA/DGVS/000041/22 and 09/GS-2132/05/10]).

Data Availability Statement: Data and code use in analysis are available at figshare at the following link: <https://doi.org/10.6084/m9.figshare.25866679>.

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