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Pulp Fiction: Why Some Populations of Ripe-Fruit Specialists *Ateles chamek* and *A. marginatus* Prefer Insect-Infested Foods

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Abstract

Fruit pulp is an easily handled energy source for many frugivorous species but generally has little protein. Accordingly, ripe-fruit specialist primate species with diets dominated by fruit pulp risk protein deficiency. While some species use leaf and flower buds, young leaves, and arthropods as an alternative protein supplement, highly frugivorous spider monkeys (*Ateles* spp.) use protein-rich young leaves and/or fig fruits. However, not all spider monkey populations have access to abundantly available figs. Comparing infestation frequencies of fruits on trees with those eaten by spider monkeys, we tested the hypothesis that, under such circumstances, spider monkeys preferentially choose those nonfig fruits with pulp infested by insect larvae (a highly protein-rich resource). We predicted that: (i) a large proportion of plant species eaten by *Ateles* would have insect larvae-infested fruits; and (ii) *Ateles* would actively select infested fruits. We tested these predictions with *Ateles chamek* and *Ateles marginatus* on the banks of the Tapajós River, Brazil. Across a 13-month sampling period, we recorded 27 plant species in the diet of the 2 *Ateles* species. Of these, 23 (85%) had larvae-infested fruits when sampled; 11 species (40%) had high levels of individual fruits infested (35-78%). We used Ivlev Values to quantify selectivity for infested/uninfested fruits in 20 plant species. Infested fruits were positively selected in 12 species (60%), while aversion to infested fruits occurred in 4 species (20%). This covert carnivory/faunivory in spider monkeys is a largely overlooked aspect of their feeding ecology. This situation would be nearly impossible to ascertain from behavioral observations alone, showing the value of integrated, multimethod approaches. The strategy used by *Ateles* spp. on the banks of the Tapajós highlights the flexibility of primate foraging choices and the importance of indirect source of protein to ripe-fruit specialist primates.

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Introduction

Zoochory provides ecological benefits from individual to ecosystem levels (Howe, 1986). It is the most common seed dispersal syndrome for many tropical forests (Moermond & Denslow, 1983), and notably so in the tropical Americas (Fleming & Kress, 2011). Tree species with fruit adapted for zoochory often are large and abundant (Fricke *et al.,* 2013), especially in lowland rainforests (Bello *et al.,* 2015). Large-sized fruits with succulent pulp characterize such trees, and the pulp represents a large proportion of the fruit's total mass (Uriarte *et al.,* 2011). The pulp is generally rich in sugars but poor in protein and free amino acids (Table I). Apart from those of such families as the Lauraceae (Jordano, 1995) and Myristicaceae (Kato, 1995), such fruits are typically low in lipids (Simmen & Sabatier, 1996) (Table I). These nutritional limitations pose a problem for primary consumers trying to achieve a diet that is both energetically adequate and nutritionally balanced (Felton, Felton, Lindenmayer, & Foley, 2009a; Oftedal, 1991; Raubenheimer & Simpson, 1997). For example, a general estimate for primates in the tropical Americas is that they require at least 15% of crude protein in their diet (Ange-van Heugten, 2008), while known diets of large-bodied species, for example, yield at most ~8% protein (e.g., *Ateles geoffroyi* (Kuhl, 1820) and *Ateles paniscus* (Linnaeus, 1858): Hladik *et al.,* 1971; Simmen & Sabatier, 1996).

Within the atelids (Platyrrhini: Atelidae), members of the genus *Ateles* are the most specialized for eating sweet, lipid-rich ripe fruit (Di Fiore *et al.,* 2008). In comparison, the closely related woolly monkeys (*Lagothrix*) eat more sugary fruits, but include a higher proportion of ripe seeds and, especially, arthropods in their diets (Gonzalez *et al.,* 2016; Stevenson *et al.,* 1994). In fact, arthropod consumption may constitute up to 41% of feeding time in some populations (e.g., *Lagothrix lagothricha lugens*; Cifuentes *et al.,* 2013). The other two remaining large atelids, muriquis (*Brachyteles*) and howler monkeys (*Alouatta*), include large proportions of leaves in their diet; some howler monkey species have fruits as a secondary (Julliot & Sabatier, 1993; Simmen & Sabatier, 1996), or even primary (Dunn *et al.,* 2009; Garber *et al.,* 2015; Martins, 2008), diet component. Although atelids may switch seasonally to such items as arthropods, buds, flowers, and young leaves, species of spider monkeys generally maintain diets of up to 90% ripe fruit, whereas only 5%, on average, is devoted to seeds, bark, fungi, termitaria soil, ground soil, and other undetermined food items (Di Fiore *et al.,* 2008). Thus, while spider monkey species may be key dispersers for a number of zoochorous trees in the tropical Americas (Arroyo-Rodríguez *et al.,* 2017; Link & Di Fiore, 2006; Ponce-Santizo *et al.,* 2006), the mainstay of their diet may not allow it to attain a nutritionally balanced intake (*sensu,* Raubenheimer *et al.,* 2009).

It has been suggested that *Ateles* might address protein limitations in their diets by consuming protein-rich young leaves (Simmen & Sabatier, 1996) and protein-rich fruits (Russo *et al.,* 2005), as well as by adjusting time allocation patterns (Di Fiore & Rodman, 2001), movement dynamics, and foraging adaptations (Norconk &

Table 1 Nutritional profiles of Tropical American fruit pulps

Family, Species[a]	In the current study, taxon consumed by *Ateles* spp at the level of: ● species, ●● genus, ●●● family	Kcal (100 g)	Protein (%)	Lipids (%)	Source
A) Ripe pulp of wild *Ateles* diet fruits					
Anacardiaceae *Spondias mombin*	●	70	0.80	2.10	Instituto Brasileiro de Geografia e Estatística (1979)
Annonaceae *Rollinia deliciosa*	●●	78	0.60	0.30	Ministério da Saúde (2015)
Arecaceae *Bactris gasipaes*	●	193	2.25	7.30	Yuyama *et al.* (2003)
Chrysobalenaceae *Hirtella glandulosa*	●●●	n/a	1.58	0.03	Maruyama *et al.* (2019)
Myrtaceae *Eugenia stipitata*	●●	21	3.04	0.06	Virgolin *et al.* (2017)
Myrtaceae *Myrcia dubia*	●●●	17	0.40	0.20	Neri-Numa *et al.* (2018)
Sapotaceae *Pouteria caimito*	●●	71.36	4.97	0.15	Virgolin *et al.* (2017)
B) Ripe pulp of common, *Ateles* non-diet, fruits[b]					
Apple (*Malus domestica*, Rosaecae)		64	0.29	0.49	U.S. Department of Agriculture (2019)
Banana (*Musa paradisica*, Musaceae)		89	1.10	0.30	U.S. Department of Agriculture (2019)
Cherry (*Prunus avium* x *cerasus*, Roseaceae)		65	1.06	0.20	U.S. Department of Agriculture (2019)
Papaya (*Carica papaya*, Caricaceae)		43	0.57	0.25	U.S. Department of Agriculture (2019)
Peach (*Prunus persica*, Rosaceae)		41	0.88	0.18	U.S. Department of Agriculture (2019)

[a] In comparison, wheat yields 336 Kcal/100 g and has 10.7 protein and 1.99 lipids (U.S. Department of Agriculture, 2019), while for Brazil nut, the values are 673, 7.91, and 63.7 respectively

[b] Though such fruits may appear in the diet of captive animals

Kinzey, 1994). However, it has been proposed that such mechanisms cannot explain the patterns of nutrient intake observed, at least for the black-faced black spider monkey, *Ateles chamek* (Humboldt, 1812; Felton, Felton, Raubenheimer, *et al.,* 2009b). Individuals of this species employ a protein leverage system that maintains a stable daily protein intake while permitting total energy intake to vary as a function of the composition of available food items (Felton, Felton, Raubenheimer, *et al.,* 2009b). At the sites studied by Felton *et al.* (2009a, b) consumption of figs was key to this system, since their pollination ecology means that ripe fig fruit obligatorily contain not only the developing larvae of agaonid Hymenoptera (fig-wasps), but also the wingless males (Weiblen, 2002) and the parasitoids of both life-stages (Dsouza & Ravishankar, 2014).

Although protein content can influence food-item choice for many animals, comparisons of such content are generally made between plant species (Dasilva, 1994; Gautier-Hion *et al.,* 1984; Hemingway, 1998; McConkey *et al.,* 2002; Stevenson, 2004). Within-species comparisons are rarely made, except for fruit size (Dias da Silva *et al.,* 2020) or ontogeny related-changes (e.g., lipid and sugar content of ripe vs. unripe fruit: Masette *et al.,* 2015; Worman & Chapman, 2005; Chapman, 2005), although there are exceptions (e.g., inter-tree variation in crop size: Houle *et al.,* 2007; age-related variation in fruit nutrient content: Carlson *et al.,* 2013; 2014; Ryan *et al.,* 2013). However, insect infestation of fruits, and its capacity to raise protein levels, is rarely considered as a variable, even though it occurs quite commonly in tropical tree species, where almost all succulent fruit have some form of infesting fruit fly (Ajuja & Liedo, 1993). As many Coleoptera, Lepidoptera, and symphytic Hymenoptera (sawflies) also have larval stages that develop in fruit, a given fruit may have several invertebrate species present at one time (Devescovi *et al.,* 2015). Unfortunately, due to the differential palatability of invertebrate taxa (e.g., the capacity of some, but not others, to secrete noxious chemicals: Laurent *et al.,* 2005), the presence of multiple invertebrate species within the fruit may serve as a complicating factor during dietary analyses (Bravo, 2012; Jordano, 1987). This may complicate efforts to improve our understanding of protein intake via ingestion of insects within fruit. This particular behavior was termed "covert carnivory," and it was predicted that it would be found in other diet-specialist primate species (Barnett *et al.,* 2017). The hypothesis that primates might gain protein in this way was originally proposed by Redford *et al.* (1984), but this insight received little attention at the time. Although McGrew (2014) introduced the term “faunivory” for the ingestion of species substantially smaller than the consumer, we feel our phrasing of “covert carnivory” is both accurate and euphonious.

Protein-restricted diets may be features of primates with diets whose main elements are low in protein. Examples of these are unripe seeds (Barnett *et al.,* 2017) and fruit pulp (Simmen & Sabatier, 1996). The Pitheciinae subfamily of the Pitheciidae, which comprises of the uacaris (*Cacajao*), cuxiús (*Chiropotes*), and sakis (*Pithecia*), is an example of the former, being specialist seed predators with diets composed of 60-80% unripe seeds (Norconk, 2007). This type of resource is low in protein, because storage protein is deposited in the seed only as it nears maturity, thus leaving only harder-to-digest structural proteins available in younger seeds (Hill & Breidenbach, 1974). The solution adopted by pitheciins is to select those seeds infested with insect larvae (*Cacajao*: Ballantyne, 2018; Barnett *et al.,* 2017; *Chiropotes*: Barnett *et al*., n.d.). Such larvae can contribute up to 86% of a seed's weight (Barnett *et al.,* 2017). Given the high protein and lipid levels of larval insects (Bukkens, 1997; Table II), they are likely to provide a substantial nutrient supplement (Barnett *et al.,* 2017). For *Cacajao ouakary* (Spix 1823), Barnett *et al.* (2017) reported that 26% of species eaten for their seeds included infested seeds; together, these comprised 40.8% of seed-feeding records. Of the 19 statistically evaluated species in that study, uacaris showed active selection for 47% of infested fruit species (Barnett *et al.,* 2017).

Members of the genus *Ateles* are an example of the second group, with fruit pulp comprising up to 70% of the diet (Di Fiore *et al.,* 2008; Stevenson & Link, 2010), where protein supplements are considered to come from shoots and buds (Cant, 1990).

Insectivory is generally considered a minor component of *Ateles* diets, not in the least because *Ateles* have specializations for arboreal locomotion, such as long, curved fingers and a vestigial thumb (Nelson & Boeving, 2015). (In fact, the name "Ateles" derives from the Greek *ατελής* for "imperfect": Rosenberger *et al.,* 2008). While the hand's structure is sufficient to manipulate fruit (Dew, 2005), it may compromise the fine levels of dexterity necessary to capture free-living animals, because a full precision grip is an anatomically demanding task (Lindshield & Rodrigues, 2009). Therefore, when insectivory is reported in *Ateles* species, it is limited to a few free-living (i.e., nonembedded) species, such as of leaf-rolling caterpillars, meliponine (stingless) bees, and termites (Di Fiore *et al.,* 2008). It also is only ever considered a minor, or supplementary, diet component (González-Zamora *et al.,* 2009; van Roosmalen & Klein, 1988), although individual bouts of insectivory may be protracted (Link, 2003).

Given the diet specialization on ripe fruits with succulent pulp by the *Ateles* clade, we hypothesize that *Ateles*, like the seed specialists pitheciins, actively select infested fruits to offset protein shortfalls in their diets. It would appear that such requirements may well be met by the protein content of fig fruits, at least at some sites (Felton *et al.,* 2009a, b in Bolivia). However, there are parts of

Table II Protein and lipid values for insect taxa and developmental stages encountered in fruit pulp compared with vertebrate meat sources

Taxon	Protein (%)	Lipid (%)	Reference
Insects			
Coleopteran larvae	23.00-66.00	14.05-35.86	Xiaoming *et al.* (2010)
Dipteran larvae	59.39	12.61	Xiaoming *et al.* (2010)
Lepidopteran larvae	14.50-68.30	5.00-49.48	Xiaoming *et al.* (2010)
Vertebrates			
Beef (chest, fat removed, raw)	17.60	20.40	NEPA (2011)
Chicken (breast, skinned, raw)	21.50	3.00	NEPA (2011)
Fish (fillet, raw):	16.70	4.00	NEPA (2011)

NEPA-Unicamp, 2011 [Núcleo de Estudos e Pesquisas em Alimentação]

Amazonia where figs are rare (Berg *et al.,* 1984; Pitman *et al.,* 2001; Wittmann *et al*., 2006). At such locations, therefore, given the differences between the of ateline and pitheciin diets, the selection by *Ateles* will involve insect larvae in the pulp, rather than within seeds. Consequently, we tested the following predictions: *(i)* a considerable proportion of fruit species eaten by *Ateles* will be infested with insect larvae at the maturational stage at which they are consumed; and *(ii)* such fruit will be actively selected by *Ateles* so that they appear at a higher percentage in the diet than they do on the tree.

Methods

Study Site and Study Species

We conducted the study in two sites along the mid-Tapajós River, including the mouth of Jamanxim River, Pará State, Brazil (Fig. 1), an area where fig trees are uncommon (Pinto, 2008). We collected data along the margins of *igapó* seasonally flooded forest (*sensu,* Prance, 1979), and in the never-flooded *terra firme* forest bordering the *igapó*, using a system of predefined trails.

We studied two species of *Ateles*. Following the taxonomy of Morales-Jimenez *et al.* (2015), these were black-faced black spider monkey (*Ateles chamek*, found on the western bank of the Tapajós River) and white-cheeked spider monkey (*A. marginatus*, found on the eastern bank).

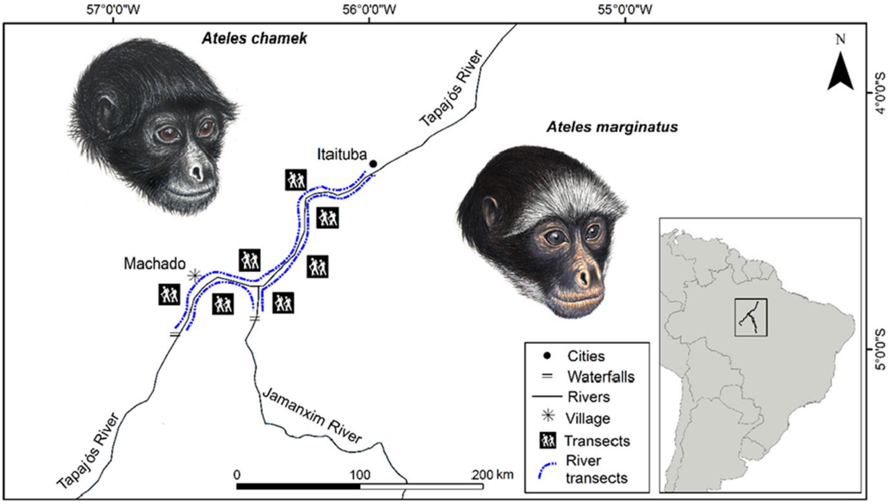

Fig. 1 Location of study site within South America (inset), positions of sampling locations at the survey site, and the presence of the two *Ateles* study species, one on either side of the Tapajós River, Brazil (main panel). *Ateles* images by Stephan Nash, and used with permission.

Data Collection

Monkeys are messy eaters (Howe, 1980), and large volumes of partially-eaten fruits generally accumulate under feeding trees. These fruits are commonly used in ecological studies (Russo, 2003; Wehncke *et al.,* 2003). To distinguish such fruits from whole ones that have been knocked down by the movements of feeding animals, or by other elements, we continue the use of the term "ort," defined as "*a fragment of food, fallen from a table. A meal remnant*" (see https://www.merriam-webster.com/dictionary/ort), first proposed by Barnett *et al.* (2017).

We performed spider monkey surveys between October 2013 and December 2014. In a survey team of two to three people, we searched for these primates between 05.30 and 18.30 hr from boats. From 06.00 to 10.00 hr and 14.00 to 18.00 hr, we searched for the monkeys on a system of seven terrestrial trails (Fig. 1), which totaled 36 km in length. Individual trail lengths were between 4 and 9 km, and were a mixture of specially cut trails and extensions to existing ones. We covered each transect three times a month. Groups were not habituated to humans, but hunting pressure is low in the region (de Oliveira *et al.,* 2016), and *Ateles* showed little fear. Nevertheless, we never approached a feeding group closer than 10 m to avoid causing the group to flee. Whenever we noted animals feeding, we recorded the feeding tree species (whenever field conditions permitted), and its GPS location. To allow the animals time to feed and for the accumulation of maximum number of ort-fruits for analysis, we did not access such feeding trees until 1-2 hours after the initial observation.

For trees that the monkeys visited, we collected samples (mean: 1.9 samples per feeding tree; SD ± 0.86, range: 1-4) of fallen, noneaten fruits (including material brought down by wind or rainstorms). We also obtained fruit samples directly from trees (mean: 1.9 samples per tree; SD ± 0.78, range: 1-3) by branch trimming. These data were obtained from a mean of 2.81 individuals per species (SD ± 1.38, range 1-7). For this, we sampled trees with fruits beneath them that had distinctive signs of very recent feeding (i.e., orts still oozing sap and not-discolored), or at which feeding had very recently been observed. We did not sample fruits that we knew from discoloration had been on the ground for more than 1-2 hours, as such fruits' insect content was likely to have been substantially reduced by foraging ants, potentially leading to erroneous conclusions.

When orts were collected from trees without direct feeding observations for *Ateles*, the potential exists for such material to be confused with the feeding remnants of other large primates in the region, such as the two *Alouatta* species present in the region (*A. nigerrima*, western bank; *A. discolor*, eastern bank: Jucá *et al.,* 2020). However, the tooth marks made by *Alouatta* and *Ateles* are distinct, and consistently so, allowing differentiation in the field.

We stored sampled material in plastic bags, labeled as either ort, fallen-uneaten, or on-tree. We added a small volume of 70% alcohol to each fruit sample bag to ensure any infestation remained contained until analyzed. This procedure ensured that seed-inhabiting larvae did not invade the pulp and bias the results.

While monkeys can be messy eaters, components found on the ground may have been discarded for a reason. It is, therefore, possible that the food remains (orts) on the ground may not truly reflect what the animals were eating. However, given that the methodological alternatives would involve marking every fruit and monitoring both their presence and any change in the variable being analyzed, several previous studies have used ort-based approaches to explore diet and selectivity patterns. These include Regan *et al.* (2001) who sampled the discarded items by *Alouatta seniculus, Ateles paniscus*, and *Sapajus apella*, as well as from the trees in which feeding occurred, Bowler and Bodmer (2011) for *Cacajao calvus ucayalii,* Gutiérrez-Granados and Dirzo (2010) who used orts to study *Ateles geoffroyi* selectivity when feeding on *Manilkara zapota* (Sapotaceae), and Julliot (1996) who used fallen, eaten, fruits when constructing a diet list for *Alouatta seniculus* and Boubli (1999) who did the same for *Cacajao melanocephalus*.

Testing Prediction I

When the collected fruit were infested, we identified all larvae present to Order. We identified trees as close to species level as possible with Gentry (1993), Ribeiro *et al.* (1999), van Roosmalen (1985), relevant volumes of *Flora Neotropica* (Pennington (1990) for Sapotaceae), and specialist treatments (Ramos (2020) for the genus *Heisteria,* Coulaceae). We used Harris and Harris (2001) and Jackson (2004) as guides to botanical terminology. We then checked our list of plant species against that of Pinto (2008) for *terra firme*, and Ferreira and Prance (1998) for *igapó*. To help in identification, we also compared common names given by local guides to those listed in Freitas da Silva *et al.* (1977, 2004). Where needed, we updated the nomenclature based on The Plant List (www.theplantlist.org). Additionally, we photographed leaves, fruits, flowers (when available), bark, and (when possible) entire trees, and later compared the images with those in virtual herbaria (Neotropical Herbarium Specimens https://www.fieldmuseum.org/node/4781; New York Botanic Garden http://sweetgum.nybg.org/science/vh/; Tropicos https://www.tropicos.org/home), as well as the Flore de Guyane site (https://floredeguyane.piwigo.com).

Testing Prediction II

To test for selectivity, we followed Felton *et al.* (2008) and Barnett *et al.* (2017) and calculated Electivity Indices (Ivlev, 1961) for each fruit species, such that:

$$\left(\mathrm{O}_i - \mathrm{T}_i\right)/\left(\mathrm{O}_i + \mathrm{T}_i\right)$$

Where O_i = percent of ort-fruit insect-infestation, and T_i = percent of on-tree fruit insect-infestation (in fruits at the same maturation level as those eaten by *Ateles* spp.). Electivity values may range from −1 to +1, with −1 indicating complete avoidance, 0 indicating no preference, and +1 indicating complete selection.

For comparative purposes, and to provide a conservative selection estimate, we used the same categories as Barnett *et al.* (2017): values falling between −0.3 and +0.3 were taken as showing no selection was occurring; the selection was considered active when values were larger than 0.33. Finally, values smaller than −0.33 indicate negative selection (i.e., active avoidance).

Ethical Note

All research complied with Brazilian law. Institutional Animal Care and Use Committee consent was not sought as data collection was ad hoc, non-invasive, and purely observational. We adhered to Association for the Study of Animal Behaviour guidelines for research animal treatment (ASAB, 2012), to the Code of Best Practices for Field Primatology of the American Society of Primatologists and International Primatological Society (www.asp.org/resources/docs/Code%20of_Best_Practices%20Oct%202014.pdf). We did not trap or handle study animals, and maintained a minimum 2-m distance from individuals to minimize stress. None of the authors have a conflict of interest to declare.

Data Availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Results

We analyzed 2,836 fruits from 74 trees, representing 27 species in 21 genera and 14 families. The samples included 1,525 (53.8%) fruits from trees and 1,311 (46.2%) orts. We sampled 34 trees by direct observation, and sampled 40 more trees where feeding had occurred very recently (i.e., fruit not discolored, and/or covered in ants). In addition, we recorded four species (*Cordia* sp., Boraginaceae; *Protium* sp. Burseraceae; *Dimorphandra* sp. and *Swarzia* sp., both Fabaceae-Caesalpinioideae) consumed by *Ateles* in *igapó* forest, but which we could not sample for logistical reasons. All records represent data from the two spider monkey species combined (Table II).

We observed *Ateles chamek* and *A. marginatus* feeding on a combined total of 31 species. Of these, we collected samples of fruit from the trees of 27 of these species. We also collected orts for 20 of the 27 species. Four of the 27 species were eaten whole and so orts could not be collected, while three had no recorded infestation.

We found that 23 species of fruits (85%) consumed by *Ateles* were infested with insect larvae at the maturational stage at which *Ateles* ate them, supporting *prediction I*. In 11 species (40.7%), high levels of individual fruits (35-78%) were infested (Table III). Partially supporting *prediction II*, we found that for the 20 species for which we had collected orts of fruits, 12 showed positive selection of infested fruits (60%), 4 showed aversions to infested fruits (20%), while no form of selection (e.g., infested and uninfested fruits were eaten at levels similar to their availability) appeared to be occurring for the four remaining species (20%; Table III).

Table III Forms of selectivity of infested fruits, where a higher percentage of infested fruits in the count of orts (fallen partly-eaten fruits) than the percentage of infested fruit on the tree is taken as an indication of selection for infested fruits by feeding spider monkeys (*Ateles chamek* and *A. marginatus*)

Family/species	No. trees	Habitat[a]	% infested on tree - all trees combined: no. infested/no. uninfested (rounded percentage)	% infested in diet - all trees combined: no. infested/no. uninfested (rounded percentage)	Ivlev Electivity Index value	Form of selection
Anacardiaceae *Spondias mombin*	2	Abandoned human cultivation	11/47 (23)	47/82 (58)	0.42	Positive
Anonaceae *Duguetia* cf. *alata*	3	Igapó	5/19 (26)	6/10 (60)	0.39	Positive
Xylopia cf. *fructescens*[c]	2	Igapó	26/98 (27)	3/52 (6)	−0.64	Avoidance
Arecaceae *Bactris gasipaes*	2	Abandoned human cultivation	13/37 (23)	39/51(77)	0.54	Positive
Burseraceae *Tetragastris altissima*	2	Terra firme	14/46 (30)	17/23 (74)	0.41	Positive
Coulaceae[b] *Heisteria spruceana*	4	Igapó	6/26 (23)	11/17 (65)[g]	0.47	Positive
Chrysobalenaceae *Licania canescens*	5	Terra firme	25/89 (28)	37/53(70)	0.43	Positive
Fabaceae *Inga alba*[c]	2	Abandoned human cultivation	72/199 (36)	2/107 (2)	−0.90	Avoidance
Inga heterophylla[c]	1	Terra firme	36/120 (30)	3/78 (4)	−0.76	Avoidance
Inga marginata[c]	4	Abandoned human cultivation	19/43 (44)	0/52 (0)	−1.0	Avoidance
Humiriaceae *Sacoglottis guianensis*	3	Terra firme	7/26 (27)	19/31 (61)	0.37	Positive
Meliaceae *Guarea* sp. Moraceae	2	Terra firme	7/37 (19)	13/27 (48)	0.71	Positive
Brosimum guianense	3	Terra firme	2/78 (3)	no values[f]	n/a	-
Brosimum parinaroides	2	Terra firme	1/40 (3)	no values[f]	n/a	-
Ficus maxima	3	Terra firme	4/100[e] (4)	no values[f]	n/a	-
Ficus sp. 2	3	Terra firme	1/100[e] (1)	no values[f]	n/a	-
Myristacaceae *Iryanthera sagotiana*	3	Terra firme	0/25	0/52	n/a	-
Osteophloeum cf. *platyspermum*	1	Terra firme	0/11	0/46	n/a	-
Virola melinonii	4	Terra firme	0/36	0/114	n/a	-
Myrtaceae *Eugenia* cf. *pseudopsidium*	7	Igapó	9/68 (13)	6/37 (16)[g]	0.10	None
Passifloraceae *Passiflora* cf. *costata*	5[d]	Igapó	22/28 (79)	16/22 (73)	-0.03	None

Table III (continued)

Family/species	No. trees	Habitat[a]	% infested on tree - all trees combined: no. infested/no. uninfested (rounded percentage)	% infested in diet - all trees combined: no. infested/no. uninfested (rounded percentage)	Ivlev Electivity Index value	Form of selection
Sapotaceae *Chrysophyllum* sp.	1	Terra firme	17/48 (35)	48/63 (76)	0.36	Positive
Ecclinusa sp.	2	Terra firme	21/28 (75)	74/86 (86)	0.07	None
Manilkara huberi	4	Terra firme	12/57 (21)	74/109 (68)	0.53	Positive
Pouteria bilocularis	1	Terra firme	10/35 (29)	78/111 (70)	0.42	Positive
Pouteria macrophylla	3	Terra firme	4/50 (8)	7/107 (7)	0.17	None
Pouteria gomphifolia	2	Igapó	12/40 (30)	58/83 (70)	0.40	Positive

[a] We did not regularly survey areas of abandoned areas of human cultivation. Instead, we gathered records *ad libitum* from sites near the study logistics base

[b] Formerly placed in the family Olacaceae

[c] Because *Xylopia* fruits and *Inga* pods are multi-seeded, and in-pod selection of seeds occurs, the given count is for seeds, not fruits

[d] Represents patches because these samples were vines, and the base was on a flooded riverbank

[e] Values refer to larvae in the pulpy outer layer of the receptacle, because fig pollination ecology guarantees insect presence in enclosed infructescence (see Janzen, 1979; Weiblen, 2002). Larvae in the outer part of the fruit was the metric chosen due to the symbiotic association between fig wasps and fig fruits, where females pollinate some flowers and lay eggs in others, and males never leave the fruit, thereby guaranteeing insect material in a fig. Thus, if the primates were choosing fruits based on insect larval presence, the pollination system guarantees some insect protein, while the presence of insect larvae in the outer layer of the receptacle would act as a variably available second dose – forming a basis on which selection could be made

[f] Fruit is small and generally ingested whole, so it was not possible to collect unambiguous orts

[g] These fruits are relatively small (1-cm diameter), and many were eaten whole. Thus, this value may be inaccurate

All infestation records involved larvae of Coleoptera, Diptera, and Lepidoptera. We found no adult insects within the fruit pulp tissues.

Discussion

We found that two species of spider monkey actively selected infested fruits across a variety of species in their diets, supporting suggestions that covert ingestion of animal protein may be a widespread feature of the *Ateles* diet (Felton *et al.*, 2008; Felton, Felton, Raubenheimer, *et al.,* 2009b). In many spider monkey populations, it appears that ingestion of animal protein would be met by eating figs, whose associations with fig wasps guarantee that a ripe fruit is an infested fruit. However, at locations (such as along the Tapajós River), where figs are rare both in numbers of species and individuals, spider monkeys instead appear to get their protein supplements from other fruits, where infestation is not a given (as it is with figs). This results in the selectivity seen in the current study.

The plant genera we recorded as diet items in this study are well-known components of the *Ateles* diet (Russo *et al.,* 2005), and the extent of insect infestation lay well within ranges reported for Amazonian fruits (Jesus-Barros *et al.,* 2012). However, the response of the study species to fruit infestation was non-uniform. Although spider monkeys selected infested fruits of some species (e.g., species within the genera *Licania, Spondias, Tetragastis*), they appeared to strongly avoid infested fruits within the genera *Inga* (Fabaceae-Mimosoideae) and *Xylopia* (Annonaceae)—both of which have multiseeded pod-like fruit. An individual selection of uninfested seeds occurred in each case, with infested seeds (and often those adjacent to them) avoided. We do not know whether such avoidance results from the infesting insects producing inimical or unpleasant-tasting chemicals or whether the specific area was made unpalatable by chemicals deposited by the host plant (Kaplan *et al.,* 2008). Although we only analyzed infestation of the sarcotesta in this study, infested seeds of both *Inga* and *Parkia* (members of the same legume subfamily) were avoided by *Cacajao* (Barnett *et al.,* 2017).

Seeds of the plant family Annonaceae are very toxic (a fact well-known to the rural Amazonians who grind them up for use as an insecticide: de Cássia Seffrin *et al.,* 2010). *Xylopia* fruits are small, single-seeded, and with a thin covering of pulp. Thus, their infestation by small dipteran larvae may have activated some defensive response in the seed, making the infested seed/pulp assemblage unpalatable to primates. This, indeed, reflects a broader methodological problem because (except here for *Xylopia* and for *Inga*, which also were eaten by *Chiropotes*), we did not check whether seeds of eaten fruits also were infested. Infested seeds may have influenced our findings and may explain some of the results where negative selection (avoidance) occurred, as any larvae in the seeds might have changed fruit pulp chemistry (or resulted in the plant changing such chemistry). Such an effect may also explain observations that *Ateles geoffroyi* avoided seeds of *Dialium* (Fabaceae-Caesalpinioideae) when infested with beetle larvae (Benítez-Malvido *et al.,* 2016).

The three analysed members of the Myristacaceae (*Iryanthera, Osteophloeum*, and *Virola*) were the only species to have no infestation of the analysed part (the aril), which may be linked to the high levels of insecticidal compounds present in these tissues (Nakamura *et al.,* 1988; Su, 1989). For four of the analysed species, the spider monkeys showed neither preference nor avoidance. These four species contained the highest (*Passiflora* cf. *costata*, 78.6%) and lowest (*Pouteria macrophylla*, 8%) infestation values. Thus, it is possible that, in scenarios of both very high and very low infestation, the gain in protein intake derived from selecting infested fruit is not offset by the extra energy and time required to achieve such gains (Krebs *et al.,* 1977); because (i) noninfested fruits are rarely encountered when fruits have high levels of infestation, so the time spent rejecting them may not be recuperated by the opportunity cost that the next fruit will be infected, while (ii) in situations where infested fruits are rare, searching for them may involve more expenditure of more energy than accrues from the ingestion of insect larvae in occasionally encountered infested fruit. This makes this an example of "hunting by expectation" (Hodges, 1981), a situation also known for nectar feeding with tamarins (*Saguinus mystax* and *Saguinus fuscicollis*: Garber, 1988). Thus, while it is important to consider the nutrient-balancing framework of primate foraging decision-making (Raubenheimer *et al.,* 2009, 2015), this and optimality are complimentary, because spatially aggregated foods must be found and then, once located, distinguished between for the highest nutrient reward with the lowest time/energy expenditure.

One of the potential limitations of the ort fruit collection method is that primates can be highly selective in their consumption of plant foods/plant parts. Thus, while large amounts of potential food may fall to the ground, at least some of this may have been discarded for a reason, which may result in an over-representation within available orts of foodstuffs in the rejected category. Given that unambiguous quantification under such circumstances would require numbering every fruit or leaf, followed by regular monitoring of their presence and the status of the variable of study interest (phytochemical composition, insect infestation, etc.), it is common to use ort-based methods to explore diet and selectivity patterns (Barnett *et al.,* 2017: *Cacajao ouakary*; Bowler & Bodmer, 2011; *Cacajao calvus ucayalii;* Boubli, 1999: *Cacajao melanocephalus*; Gutiérrez-Granados & Dirzo, 2010: *Ateles geoffroyi*; Julliot, 1996: *Alouatta seniculus*; Regan *et al.,* 2001: *Alouatta seniculus, Ateles paniscus* and *Sapajus apella*; Take, 2017: *Pithecia chrysocephala*, *Saimiri sciureus* and *Saguinus bicolor*). Until a nontime- and nonlabor-intensive method for monitoring whole canopies and their fruits or leaves becomes available, studies are likely to continue with this potential, and currently unquantifiable, bias as an inherent constituent.

Consumption of larval insects is an especially efficient means of accessing protein, which can be 60-80% by wet weight (Bukkens, 1997), as well as a variety of free amino acids (Drew, 1988), lipids, and minerals (Finke, 2013). In addition, accessing such insects is energetically efficient since larvae, generally being more lightly sclerotized, often are easier to digest than fully developed individuals (imagoes) (Raubenheimer & Rothman, 2013). Furthermore, the use of such larvae can be energetically effective as they can form a spatially aggregated resource, unlike free-living imagoes that often are dispersed or may have defensive behaviors.

There are, however, potential downsides to ingesting infested fruits. For example, if fruit infestation is extensive, or large volumes of the fruit have already been ingested by larvae, the energetic and nutritive values of infested fruits may be lower than comparably sized noninfested ones. This point has been used to explain why infested fruits are sometimes avoided by rodents (Muñoz & Bonal, 2008; Steele *et al.,* 1996), and bats (Utzurrum & Heideman, 1991). In addition, damaged plant tissues may become toxic due to fungal infection. Such toxicity is hazardous, as some spoilage fungi synthesize toxic molecules, such as aflatoxins and patulin, which are some of the most potent carcinogens known (Janzen, 1977). Thus, spoilt fruits (discolored or blotched) are widely avoided by frugivores (Borowicz, 1988; Buchholz & Levey, 1990). This, and changes in palatability due to accumulation of excretory products and alteration of chemosynthetic pathways (Tollrian & Harvell, 1999), may explain other examples of frugivores avoiding infested fruits (primates: Bravo, 2012; Julliot, 1996; bats: Engriser, 1995; birds: Palacio *et al.,* 2020; Traveset *et al.,* 1995). However, some cases of avoidance appear to be due to the direct influence of the infesting insect. For example, larvae of the holly berry midge (*Asphondylia ilicicola,* Cecidomyiidae) chemically prevent the berry of the American holly (*Ilex opaca*, Aquioliaceae) from turning red, which results in avoidance of infested fruits by avian frugivores that use red as a cue for edibility (Krischik *et al.,* 1989). All of these potential downsides and complex mutualisms indirectly affect plant-consumer interactions (Krischik *et al.,* 1989), which may be responsible for the non-uniform responses of ripe-fruit specialists to fruit infestation.

There also is the peculiar case of figs (genus *Ficus*); their pollination ecology involves fig-wasps (Agaonidae), with larvae of both sexes developing in the maturing synconium. Having fertilized females, the wingless males die without leaving the fruit (Janzen, 1979; Weiblen, 2002). Thus, consumption of wild fig fruits inevitably involves covert carnivory (*sensu,* Barnett *et al.,* 2017) of, at least, dead male and developing larval wasps. Even though the fig-agaonid wasp relation is biologically well known, the nutritional significance of the concealed larval component of the fruit is rarely (Link, 2003) commented on or acknowledged, even when figs make up truly significant parts of the diet (e.g., hornbills, primates: Choudhury, 1989; Kinnaird & O'Brien, 2005; Kinnaird *et al.,* 1996; Wrangham *et al.,* 1993). It is therefore pertinent to note that figs are a major component of *Ateles* diets in certain parts of their geographic range (e.g., 50% for *A. chamek* in Bolivian semihumid forests: Felton *et al.,* 2008).

With the exception of fig wasps, their braconid parasites, and some gall-forming wasp species (Dsouza & Ravishankar, 2014; Weiblen, 2002), it seems unlikely that covert carnivory is a contributory component in figs, because very few species of insect appear to infest figs on the tree. Fallen figs are rapidly colonized by yeasts, beetles, and flies (Palmieri & Pereira, 2018), but *Ateles* spp. rarely forage on the ground (Campbell *et al.,* 2005), so that this infestation is unlikely to be relevant to spider monkeys. Additionally, although they represent one of the major groups of fruit-infesting insects in the tropics (Ajuja & Liedo, 1993), *Anastrepha* fruit flies (Tephritidae) are not known to infest wild figs (Hernández-Ortiz & Pérez-Alonso, 1993; Jesus-Barros *et al.,* 2012). This is likely due to the presence of digestive enzymes (ficins) with strong larvicidal properties (Kitajima *et al.,* 2018) in the latex of many Moraceae (Zare *et al.,* 2013).

Nutritional modelling of protein requirements of a Bolivian population of *A. chamek* (Felton, Felton, Wood, *et al.,* 2009c) matched observed protein intake and nutritional profiles closely, so that Felton and coworkers concluded that *Ficus* was a nutritionally balanced food for *Ateles*. However, while eating figs is common in *Ateles* species, in no other population studied do ingestion levels reach those reported from Bolivia (Felton *et al.,* 2008, 2009a,b,c), where almost 50% of total time spent feeding involved ingesting figs. This may reflect underlying differences in study site floral composition, where four *Ficus* species occurred, two of which (*Ficus boliviana, Ficus trigona*) were common and produced large fruit crops for 8–9 months/year, so providing fruits when other trees did not (Felton et al., 2008; Felton, Felton, Wood, *et al.,* 2009c). In contrast, in the Tapajós National Forest (a protected area close to the current study sites), two independent studies (de Lima Francisco & Cordeira, 2004; Pinto, 2008) reported only one (uncommon) *Ficus* species. The high level of *Ficus* ingestion reported by Felton *et al.* (2008) appears unusual, as a comparison of sites in Surinam, Ecuador, Colombia, and Panama found *Ficus* comprised no more than 15.4% of the diet at the individual sites and, at two sites, less than 3% of the diet (Russo *et al.,* 2005).

That very few figs were consumed at our study sites may simply be because figs are not common enough in Tapajós basin forests for their fruits to dominate the diet of large-bodied primates travelling in large groups (30-50 individuals: Symington, 1990). Nevertheless, given the importance of phylogeny in determining physiology (Garland Jr. *et al.,* 2005; Herrera, 1992a), and the metabolic underpinning of overall ecology in a genus (Herrera, 1992b; McNab, 2002), it is very likely that the protein-balancing metabolic model advanced by Felton *et al.* (2008) is practiced by *A. chamek* and *A. marginatus* on the Tapajós, but that, in the absence of large volumes of nutritionally-balanced figs, these primates adopt a strategy of selecting infested fruits as an energetically efficient alternative. This hypothesis could be tested on other spider monkey populations in forests of varying *Ficus* abundance.

Thus, while we have shown that two members of the genus *Ateles* practice covert carnivory, it is possible that other species, generally considered highly frugivorous, also may adopt this strategy. Accordingly, we suggest that researchers check the pulp (or seeds) being eaten for such evidence. Other sources of insects that merit investigation, include the leaf bases of epiphytic bromeliads, buds of leaves and flowers (see Barnett *et al.,* 2020 for infestation levels of *Eschweilera* flower buds), and young leaves. Spider monkeys use bromeliads as a water source (Di Fiore *et al.,* 2008), for their succulent leaf bases (Campbell, 2008; Dew, 2005), or for the small vertebrate prey they conceal (Valero, 2004). However, they also contain larvae of a specialist genus of bromeliad-eating weevils (*Metamasius*, Dryophthoridae: Cave *et al.,* 2006), which could provide an additional reason for their exploitation. Buds also should be considered due to the ubiquity of bud-boring insect larvae (Sugiura & Yamazaki, 2009) and, while young leaves are widely considered a good source of protein (Felton *et al*., 2008; Felton, Felton, Wood, *et al.,* 2009c), they are commonly attacked by leaf-mining insects (Sinclair & Hughes, 2010), which could contribute supplemental levels of protein, as could the insects within phytophilous galls (Askew, 1980; Raman, 2012).

Further complexities arise because a species may select infested fruit from one plant species but not another (e.g., common bush tanagers, *Chlorospingus ophthalmicus*: Valburg, 1992; black-and-gold howler monkeys, *Alouatta caraya*: Bravo, 2012; Bravo & Zunino, 1998; golden-backed uacaris, *Cacajao ouakary*: Barnett *et al.,* 2017). This likely results from the heterogeneity of plant responses, including those where plants selectively deposit toxic compounds into infested fruits (Ibanez *et al.,* 2009), as well as insect countermeasures where larvae sequester such compounds for their own defense (Ferro *et al.,* 2006). Just as such higher-order interactions (*sensu,* Mayfield & Stouffer, 2017) finesse our view of both potential seed predators (Barnett *et al.,* 2012, 2017; Herrera, 1989), it also may do so with seed dispersers, because ingestion of seed- or pulp-eating insects generally destroys them (Bravo, 2008; Herrera, 1989; Jordano, 1987), although there are some exceptions (Di Iorio, 2015). In situations where such seed- or pulp-eating insects are destroyed during ingestion, there is reduction in the overall population of organisms that can depress plant reproductive success (da Silva & Pinheiro, 2009; Wilson, 2008); however, in some cases selective predation on insect-infested fruits leads to the destruction of the fruits (Scott & Black, 1981).

As a caveat, because spider monkeys often ingest fruit whole (Russo *et al.,* 2005), discarded parts of a fruit might be those that were overripe or immature, potentially leading to erroneous estimates of selectivity. This possibility should be tested, either in the wild (where it would be observationally challenging—although perhaps resolved by camera traps in favored fruiting trees, with premarked fruit) or in captivity with choice tests of fruits of known infestation levels.

Plant species generally have multiple seed dispersers (Willson & Traveset, 2000; Zamora, 2000), and these may not react in the same way to infesting insects: some may prefer infested fruits or seeds, while others avoid them (Barnett *et al.,* 2017; Valburg, 1992). Passage through *Ateles* guts rarely kills seeds and, indeed, often enhances germination rates (see Fuzessy *et al.,* 2016 for topic review). Thus, by eating insect-infested fruit that other species might refuse, spider monkeys ensure that individual fruits that might otherwise not be dispersed achieve a zoochoric interaction, enhancing the plants reproductive potential. In addition, our study shows that, for some populations at least, *Ateles* engage in active insectivory, via the selection of infested fruits. Given the elegant interplay Felton *et al.* (2009a, b, c) demonstrated between energy intake and diet item composition, and the central role of protein as a key element in macronutrient balancing, it is possible that distinct frugivore populations do things differently, with the abundance of protein-rich resources in the region inhabited by different study populations, as the main variable. This may parallel the differences observed in time spent foraging for nonembedded arthropod prey displayed by different species and populations of *Lagothrix* (Gonzalez *et al.,* 2016), the ateline genus closely related to *Ateles* (Ange-van Heugten, 2008), because our findings reinforce the observation of Felton *et al.* (2008, p. 393) that "both intra- and interspecific distinctions in ateline feeding ecology are best explained by differences in the local food resources" (see also Russo *et al.,* 2005). Thus, studies comparing the incidence of covert carnivory in areas where figs either do or do not constitute significant parts of the diet of resident *Ateles* would both clarify the current situation and help open future avenues of research, as well as providing larger samples for genera such as *Xylopia*, where numbers of sampled individuals were low in the current study. Because a particular stage of fruit ripeness generally corresponds to a particular insect maturation stage, future studies could investigate whether infesting insect species, and if their different life cycles influence protein/lipid/micronutrient availability for individual fruit species. Additional studies could investigate how variation in fruit morphology and size affects insect infestation.

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