


# Beans with bugs: Covert carnivory and infested seed selection by the red-nosed cuxiú monkey

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## Abstract

Members of the Neotropical primate genus *Chiropotes* eat large volumes of immature seeds. However, such items are often low in available proteins, and digestion of seeds is further inhibited by tannins. This suggests that overall plant-derived protein intake is relatively low. We examined the presence of insect larvae in partially eaten fruits, compared with intact fruit on trees, and examined fecal pellets for the presence of larvae. We found that red-nosed cuxiú (*Chiropotes albinasus*) individuals may supplement their limited seed-derived protein intake by ingesting seed-inhabiting insects. Comparison of fruits partially eaten for their seeds with those sampled directly from trees showed that fruits with insect-containing seeds were positively selected in 20 of the 41 *C. albinasus* diet items tested, suggesting that fruits with infested seeds are actively selected by foraging animals. We found no differences in accessibility to seeds, that is, no differences in husk penetrability between fruits with infested and uninfested seeds excluding the likelihood that insect-infestation results in easier access to the seeds in such fruits. Additionally, none of the *C. albinasus* fecal samples showed any evidence of living pupae or larvae, indicating that infesting larvae are digested. Our findings raise the possibility that these seed-predating primates might provide net benefits to the plant species they feed on, since they feed from many species of plants and their actions may reduce the populations of seed-infesting insects.

Abstract in Portuguese is available with online material.

## KEYWORDS

bearded saki, pitheciid, protein, seed predation, tannin

## 1 | INTRODUCTION

The family Pitheciidae represents, “a clade more committed to eating seeds than any other primate group” (Rosenberger, 2020; 53). This is especially true of the sub-family Pitheciinae, which comprises three genera (*Cacajao*, *Chiropotes*, and *Pithecia*) all of which show notable dental and cranial specializations for accessing and extracting seeds from non-pulpy, hard-husked fruits (Kinzey, 1992; Püschel et al., 2018). Of these genera, *Cacajao* and *Chiropotes* have the most derived suite of adaptations for such a diet (Kinzey, 1992; Rosenberger, 2020). In addition, the annual diets of both genera are often dominated by seeds from immature, rather than ripe, fruits (Ayres, 1989; Barnett et al., 2012; Norconk, 2020; Norconk et al., 2013; Pinto et al., 2020). In the genus *Chiropotes*, such immature seeds may represent between 33% and 75% of the diet (Table 1). These seeds may be contained within fruits with either dry or pulpy husks (pericarp/mesocarp). Fruits of 117 plant species were reported by Pinto (2008) as being eaten by *C. albinasus*, of these 66 (52.8%) were dry-husked, the remainder having pulp. Whether possessing pulp or not, most fruit species are used for their seeds (53% and 75% of diet for the two sites reported on by Pinto et al., 2018), with the seeds eaten when unripe (e.g., 48 and 65%, respectively; Pinto et al., 2018).

Exploitation of such seeds is beneficial in that unripe fruits are available for longer periods than ripe ones (Boubli, 1999; Norconk, 2020; Shaffer, 2013), and feeding competition with other species may be reduced (e.g., *Ara* macaws, Palminteri et al., 2012; other primates, Kinzey & Norconk, 1990). However, seed-eating presents potential nutritional challenges, since unripe seeds tend to be rich in hard-to-metabolize structural proteins and poor in the more easily digested storage proteins (Craig, 1988), which are generally deposited shortly before dispersal (Gallardo et al., 2008; Harborne, 1996; Table 2).

Tannin protein-binding capacities may also provide a nutritional challenge to seed eaters. Tannins are commonly present in high concentrations in both unripe fruit pulps and seeds (Harborne, 1996). While tannin-rich food items are often avoided due to their astringency (Marks, 1986; Simmen & Charlot, 2003), that tannins bind with proteins may also pose a challenge (Hagerman, 1989), since this subsequently render such proteins unavailable for digestion thus reducing food quality (Glander, 1982; Robbins et al., 1987). The relationship between tannin ingestion and their potential negative effects is complex (Felton et al., 2009). While proline-rich proteins (PRPs) in saliva are known to bind with and detoxify tannins in some animals, it is not yet known whether pitheciins produce PRPs or if they would increase or decrease nitrogen digestibility in the gut (Skopec et al., 2004). Nevertheless, the high levels of condensed and hydrolysable tannins in the immature seeds indigested by *C. albinasus* may significantly reduce the availability of what small levels of proteins are available from them during digestion (Lambert & Garber, 1998).

Pitheciins may balance the risks of ingesting high concentrations of tannins and toxins by ingesting a variety of fruits with

different chemical compositions (Felton et al., 2009; Righini, 2017; AA Barnett, unpublished data), although individual *Cacajao* and *Chiropotes* may still run the risk of entering protein deficiency during day-to-day foraging. Ingestion of protein-rich buds, young leaves, and insects may compensate for this (*Cacajao*: Barnett et al., 2013; *Chiropotes*: van Roosmalen et al., 1988). However, for insect ingestion only free-living insects (i.e., not those habitually inhabiting fruits, their seeds, or other food resources) such as caterpillars, ants, termites, and grasshoppers have generally been considered (Ayres & Nessimian, 1982; Frazão, 1991; Mittermeier et al., 1983; Pinto et al., 2018; Port-Carvalho & Ferrari, 2004; Veiga & Ferrari, 2006). When consumption of insects embedded in fruit or seeds is recorded, their ingestion is generally considered accidental (Raubenheimer & Rothman, 2013).

Redford et al. (1984) pointed out that seeds are often colonized by insect larvae (Coleoptera, Diptera, and Lepidoptera), providing a potential source of protein for seed-eating primates. While this observation received little attention at the time, more recent studies by Barnett, Ronchi-Teles, et al. (2017); Barnett, Silla, et al. (2017) and Ballantyne (2018) have shown that at least one pitheciin, the golden-backed uacari (*Cacajao ouakary*; sensu Ferrari et al., 2014), actively selects fruit with insect-infested seeds (termed “covert carnivory” by Barnett, Ronchi-Teles, et al., 2017; Barnett, Silla, et al., 2017).

Selective predation of infested fruits has been observed in primates (Bravo, 2012), and other vertebrates (Alves et al., 2018; Drew, 1987; Silviu, 2002; Valburg, 1992). Predation of seed-eating insects is widely considered to be beneficial to host plant fitness, since removing a section of the insect seed-predator population of future seeds effectively enhances the reproductive fitness of the individual plants (Bravo, 2008; Herrera, 1989; Jordano, 1987). Furthermore, as noted by Lambert (2001), additional benefits may result from the predation of insect-damaged seeds since such seeds often become infested by fungi and other pathogens (Barnett et al., 2012; Menendez, 2019), which can potentially transfer infestations to healthy seeds and seedlings, reducing their survivorship. Choice of infested fruits and seeds by seed-eating primates may reduce such losses, increasing overall plant reproductive fitness (Lambert, 2001). For this to occur, insect larvae and pupae must not survive passage through the digestive tract of a seed-eating primate, as survivorship could result in their dispersal (Guix & Ruiz, 1995, 1997).

Selective predation of infested fruits has not been studied in *Chiropotes*. However, as they have a dietary profile and feeding ecology very similar to *Cacajao* (Ayres, 1989; Norconk, 2020), it is plausible that *Chiropotes* may also benefit from covert carnivory. Accordingly, we present here a study of infested fruit selectivity in the red-nosed cuxiú (*Chiropotes albinasus*).

We tested the hypothesis that *C. albinasus* preferentially select fruits whose seeds are infested with larval insects, these being protein-rich (Rothman et al., 2014) and relatively easy to digest. We predicted that:

**TABLE 1** Infestation levels and selectivity<sup>a</sup> based on Ivlev Values for 45 diet items from 37 species eaten by *Chiropotes albinus* on the middle Rio Tapajós, Pará State, Brazil.<sup>b,c</sup>

Scientific name	No. of trees <sup>d</sup>	Habitat <sup>e</sup>	Part eaten and maturation state <sup>f</sup>	Tree: Infested/uninfested fruits (% on tree with infested seeds)	Diet: Infested/uninfested fruits (% in diet sample with infested seeds)	Electivity index	Selection type <sup>g</sup>
<i>Annonaceae</i>							
<i>Xylopia cf. frutescens</i>	4 <sup>h,i</sup>	Ig	Am	40/98 (40.8)	2/17 (11.8)	-0.55	A
<i>Apocynaceae</i>							
<i>Malouetia flavescens</i>	7 <sup>h</sup>	Ig	Si	27/117 (23.1)	28/37 (75.7)	0.53	P
<i>Malouetia flavescens</i>	3	Ig	Sm	9/46 (19.6)	12/25 (48.0)	0.42	P
<i>Tabernaemontana</i> sp.	7 <sup>h,j</sup>	Ig	Si	6/28 (21.4)	12/21 (57.1)	0.45	P
<i>Tabernaemontana</i> sp.	4	Ig	Sm	5/23 (21.7)	9/14 (64.3)	0.52	P
<i>Chrysobalanaceae</i>							
<i>Licania cf. canescens</i>	2 <sup>i</sup>	Tf	Si	14/89 (15.7)	14/22 (63.7)	0.60	P
<i>Euphorbiaceae</i>							
<i>Hevea spruceana</i>	8 <sup>h</sup>	Ig	Si	7/58 (12.1)	18/40 (45.0)	0.58	P
<i>Mabea nitida</i>	3 <sup>h</sup>	Ig	Si	21/60 (35.0)	2/23 (8.7)	-0.61	A
<i>Fabaceae</i>							
<i>Inga alba</i>	5 <sup>h</sup>	Tf	Am	63/199 (31.7)	3/47 (6.4)	-0.64	A
<i>Inga heterophylla</i>	2 <sup>h</sup>	Ig	Am	46/122 (39.4)	2/50 (4.0)	-0.79	A
<i>Dalium</i> sp.	3	Ig	Pm	4/37 (10.8)	6/16 (37.5)	0.55	P
<i>Dalium</i> sp.	2	Ig	Si	9/19 (47.3)	2/16 (12.5)	-0.58	A
<i>Macrolobium acaciifolium</i>	8	Ig	Si	17/100 (17.0)	9/46 (19.6)	0.07	O
<i>Swartzia polyphylla</i>	2	Ig	W <sup>o</sup>	27/85 (31.8)	19/23 (82.6)	0.44	P
<i>Swartzia polyphylla</i>	2	Ig	Am	8/40 (20.0)	3/17 (17.7)	-0.06	O
<i>Humiriaceae</i>							
<i>Endopleura uchi</i>	1 <sup>i</sup>	Tf	Pi	4/31 (12.9)	2/19 (10.5)	-0.10	O
<i>Lecythidaceae</i>							
<i>Couratari stellata</i>	2	TF	Sm	22/207 (10.6)	5/44 (11.7)	0.05	O
<i>Couratari cf. tenuicarpa</i>	3	Ig	Si	16/221 (7.2)	4/52 (7.7)	0.03	O
<i>Couratari cf. tenuicarpa</i>	2	Ig	Sm	24/194 (12.4)	6/63 (9.5)	-0.13	O
<i>Eschweilera albiflora</i>	5 <sup>h</sup>	Ig	Si	28/74 (37.8)	34/49 (79.6)	0.36	P
<i>Eschweilera obversa</i>	3 <sup>h</sup>	TF	Si	61/227 (26.9)	57/94 (60.6)	0.43	P
<i>Lecythis lurida</i>	1 <sup>h</sup>	TF	Si	55/80 (67.8)	20/37 (54.1)	-0.11	O
<i>Menispermaceae</i>							
<i>Abuta cf. panurensis</i>	1	TF	Pm <sup>k</sup>	7/34 (20.6)	26/41 (63.4)	0.51	P
<i>Moraceae</i>							
<i>Brosimum parinarioides</i>	3 <sup>i</sup>	Tf	Wm	2/78 (2.6)	-	-	n/a
<i>Myristicaceae</i>							
<i>Iryanthera sagotiana</i>	1	Tf	Am	0/23	-	-	n/a
<i>Myrtaceae</i>							
<i>Calyptanthes</i> sp.	5 <sup>i</sup>	Ig.	Si	14/34 (41.2)	17/27 (62.9)		P
<i>Calyptanthes</i> sp.	3 <sup>i</sup>	Ig	Wm	26/35 (74.3)	-	-	n/a
<i>Eugenia</i> sp.	11 <sup>i</sup>	Ig	Si	82/100 (82.0)	36/47 (76.6)	-0.03	O
<i>Eugenia</i> sp.	4 <sup>i</sup>	Ig	Wm	36/50 (72.0)	-	-	n/a

(Continues)

TABLE 1 (Continued)

Scientific name	No. of trees <sup>d</sup>	Habitat <sup>e</sup>	Part eaten and maturation state <sup>f</sup>	Tree: Infested/uninfested fruits (% on tree with infested seeds)	Diet: Infested/uninfested fruits (% in diet sample with infested seeds)	Electivity index	Selection type <sup>g</sup>
<i>Olacaceae</i>							
<i>Chaenochiton loranthoides</i>	4	Ig	Si	12/52 (23.1)	13/19 (68.4)	0.49	P
<i>Passifloraceae</i>							
<i>Passiflora</i> cf. <i>costata</i>	5 <sup>ij</sup>	Ig	Pm, Sm	10/29 (34.5)	8/11 (72.3)	0.35	P
<i>Polygalaceae</i>							
<i>Moutabea guianensis</i>	5 <sup>il</sup>	Tf	Si	14/63 (21.5)	19/33 (57.6)	0.46	P
<i>Securidaca</i> sp.	3			78/100 (78.0)	21/29 (72.4)	-0.03	O
<i>Rubiaceae</i>							
<i>Duroia</i> sp.	7	Ig	Wi	4/47 (8.5)	2/16 (12.5)	0.19	O
<i>Duroia</i> sp.	4	Ig	Wm	4/34 (11.8)	2/19 (10.5)	-0.05	O
<i>Salicaceae</i>							
<i>Casearia</i> sp.	3 <sup>m</sup>	Ig	Wm	39/56 (69.6)	9/15 (60.0)	-0.07	O
<i>Sapotaceae</i>							
<i>Chromolucuma</i> cf. <i>rubriflora</i>	2 <sup>m</sup>	Ig	Si	25/43 (58.1)	39/61 (63.9)	0.05	O
<i>Chrysophyllum</i> sp.	2 <sup>m</sup>	TF	Si	14/49 (28.6)	22/31 (70.1)	0.42	P
<i>Elaeoloma glabrescens</i>	3 <sup>m</sup>	Ig	Si	8/29 (27.6)	15/23 (65.2)	0.41	P
<i>Manilkara bidentata</i>	2 <sup>m</sup>	Ig	Si	11/44 (25.0)	54/86 (62.7)	0.40	P
<i>Pouteria bilocularis</i>	1 <sup>m</sup>	Tf	Si	13/35 (37.1)	7/20 (35.0)	-0.03	O
<i>Pouteria</i> cf. <i>cuspidata</i>	1 <sup>m</sup>	Ig	Si	19/64 (29.7)	36/56 (64.3)	0.36	P
<i>Pouteria gomphiiifolia</i>	3 <sup>m</sup>	Ig	Si	17/41 (41.5)	22/27 (81.4)	0.32	P
<i>Pouteria</i> cf. <i>macrophylla</i>	2 <sup>m</sup>	TF	Si	39/50 (78.0)	21/28 (75.0)	-0.02	O
<i>Theaceae</i>							
<i>Ternstroemia</i> <sup>n</sup> <i>candolleana</i>	1	Ig	Si	8/27 (29.7)	25/39 (64.1)	0.37	P

<sup>a</sup>Electivity Index =  $(O_i - T_i)/(O_i + T_i)$ . Electivity Index data are given for each diet item and is based on all analyzed individuals of the species concerned for which a particular morphological part was consumed. If a different part was consumed, and that was the only part ingested, then that was treated as a separate diet item from any others of the same species (e.g., whole young pods and arils from mature pods of *Swartzia polyphylla*). If the same part was eaten at two different maturational stages (e.g., seeds from immature and mature fruits of *Malouetia flavescens*), this too was treated as two distinct diet items, and the electivity indexes calculated separately combined (different maturation states treated separately).

<sup>b</sup>*C. albinasus* was seen feeding on seeds of three species of tree that could not be sampled for logistical reasons (*Acosmium* sp., *Aldina* [*heterophylla*?], *Swartzia* sp., all Fabaceae).

<sup>c</sup>*C. albinasus* was also seen eating flowers and young leaves, these data will be reported elsewhere.

<sup>d</sup>In all eight cases of multi-use, the same trees were visited.

<sup>e</sup>Habitat: Tf = *terra firme*, Ig = *igapó*.

<sup>f</sup>Part eaten: A = aril/sarcotesta, P = pulp, S = seed, W = whole fruit, maturation state: m = mature, i = immature.

<sup>g</sup>Selection type: P = positive, A = avoidance, and O = none; where species that were avoided had some fruits with infested seeds (or fruit parts eaten), these were always very lightly infested, so that it is possible that any induced zootropic phytochemicals may not have been present or were present at very low levels.

<sup>h</sup>Multi-seeded fruits, selectivity estimated for individual seeds.

<sup>i</sup>Fruit species had a pulpy pericarp, and there was insect infestation in both the pericarp and seeds.

<sup>j</sup>A vine with N = number of clumps; the vine was growing on a flooded bank at the time of feeding.

<sup>k</sup>In this species, the layer of pulp is thinner as than the exocarp is thick, and infesting insects appeared to be feeding on both.

<sup>l</sup>A vine, but the true number of individuals was not ascertained.

<sup>m</sup>Fruit species had a pulpy pericarp, and there was insect infestation only in the seeds.

<sup>n</sup>The genus *Ternstroemia* considered by some to belong to the Pentaphylaceae (or its own family Ternstromeaceae).

<sup>o</sup>Very immature pods.

TABLE 2 Content of red-nosed cuxiú (*Chiropotes albinus*) fecal pellets, Rio Tapajós, Pará State, Brazil.

Pellet #	Plant material present	Animal material present	Comments
1	Pollen, leaf frag, stamens	Some legs (of beetles?), beetle elytra	-
2	No identifiable material	Spiders, caterpillar headcapsules, setae	Possible consumption of the same kind of caterpillars as reported by Veiga and Ferrari (2006)
3	No identifiable material	No identifiable material	No identifiable remains, gray-pink matrix appeared smooth and homogeneous
4	Strands of fiber (palm fruit?)	Spiders, beetle elytra (some very small)	Very small elytra could be from seed beetles (Bruchinae)
5	No identifiable material	Winged ant remains (~25% of pellet by volume)	Based on thorax fragments, ants would have been around 1.25 cm long. Ferreira et al. (2021) report ant-eating very common in South American primates.
6	Three intact <i>Duroia</i> seeds, plus testa fragments	No identifiable remains – some material that might be larval skin	Two seeds germinated <sup>a</sup>
7	No identifiable material	Beetle wings and elytra (some very small), spiders, termite wings.	As above, possible bruchinids from seeds?
8	Possible bud scales, pollen, a petal fragment	Remains of several stingless bees, small irregular shapes (possible remnants of nest resin)	Moura (2016) reports <i>Chiropotes sagulatus</i> raiding stingless bee nests
9	Leaf fragments, bud scales (?)	Leg fragments (possibly from beetle imagos)	Young leaf?
10	No identifiable material	Some termite wings, beetle legs, and elytra (some very small)	As above, possible bruchinids?
11	-	-	No identifiable remains, gray-pink matrix appeared smooth, and homogeneous
12	No identifiable material	Grasshopper remains; dense, non-plant, material – possibly from a spider egg case?	Spider egg case eating reported by Moura (2016) for <i>Chiropotes sagulatus</i>
13	-	-	No identifiable remains, pinkish-gray matrix appeared smooth, and homogeneous

<sup>a</sup>Three *Duroia* seeds were found intact in one pellet. Since previous studies had found *D. velutina* seeds in germinated from feces of *Cacajao*, a close *Chiropotes* relative (Barnett et al., 2012), the seeds were placed on local soil in a plastic pot covered with netting, and watered to keep the soil moist, two seeds sprouted (9 and 11 days after sowing).

- (i) a high percentage of the fruits eaten by *Chiropotes albinus* would be infested by larval insects;
- (ii) foraging *C. albinus* would select such infested fruits at a frequency disproportionate to their availability;
- (iii) fruit-infesting larvae would not be found intact and alive in the feces of *C. albinus*;

Finally, because larval infestations generally create holes and tunnels in fruit pericarp and/or seed coats (see images in Barnett et al., 2016), this could, potentially, make the fruit husk, and/or that of the shell of the seed within, easier to break, resulting in a mechanical advantage to their exploitation. Thus, to test whether mechanical rather than nutritional benefits underpinned any recorded preferences, we also predicted that:

- (i) for any given species, the force needed to penetrate the protective covering of the part eaten by *C. albinus* would be less in infested than in uninfested fruits.

## 2 | METHODS

### 2.1 | Study site and species

The study took place on middle Rio Tapajós, Pará State, Brazil (Figure 1). Regionally, the main forest types are tall *terra firme* (never-flooded) forest (15–30 m), and *igapó* (Prance, 1979). The latter is a seasonally flooded forest, inundated at the study site from January-late April/early May (de Oliveira et al., 2016), by the nutrient-poor waters of the Rio Tapajós (Junk, 2013). *Igapó* forest forms a narrow strip (rarely more than 10 m wide) along the banks of the Tapajós and tributaries. The study area lies between the town of Itaituba (4°16'33"S, 55°59'02"W), the impassable rapids on the Tapajós south (upstream) of Machado village, and the first set of impassable rapids on the lower Rio Jamaxim (4°45'23"S, 56°26'15"W; Figure 1).

Unlike many primate genera in the Tapajós river basin (e.g., *Alouatta*, *Aotus*, *Ateles*, *Mico*, and *Plecturocebus*), the species of

*Chiropotes*, the red-nosed cuxiú (*C. albinasus*), is found on both banks (de Oliveira et al., 2016). The species is arboreal, weighs some 3.5 kg, travels in groups of 20–60, has a home range that may exceed 1000 ha (Pinto et al., 2020), and is listed as Vulnerable by the IUCN (Pinto et al., 2020).

## 2.2 | Data collection

### 2.2.1 | Field surveys

As part of a broader series of faunal surveys in the mid-Tapajós (de Oliveira et al., 2016; Barnett & de Oliveira 2018; Barnett, Ronchi-Teles, et al., 2017; Barnett, Silla, et al., 2017; Barnett, de Oliveira, et al., 2018; Barnett, Todd, & de Oliveira, 2018; Jucá et al., 2020; Tománek et al., 2020), we collected field data on *C. albinasus* between October 2013 and December 2014. Primate surveys occurred between 05:30 and 18:30 h from motorized canoes, and from 06.00–10.00 h and 14.00–18.00 h on trails. Using a pre-existing trail system (de Oliveira et al., 2016), we conducted primate observations and collected data on the margins of the *igapó* (a 200-km transect) and in adjacent *terra firme* forest (five 10-km transects). During these surveys, the GPS location of each feeding tree was recorded, and in-field taxonomic identification of individual trees was conducted as far as possible. When a *C. albinasus* group was seen entering a feeding tree, the group was observed to ascertain feeding bout duration, plant species identity and part eaten, and the way it was processed. As the study was part of a broader faunal study, such observations were discontinued after 30 min, unless the encounter was close to the end of a survey session.

### 2.2.2 | Sample form

Monkeys are not tidy feeders (Howe, 1986), and it is common for large volumes of partially eaten fruits to accumulate below feeding trees. Barnett, Ronchi-Teles, et al. (2017); Barnett, Silla, et al. (2017)

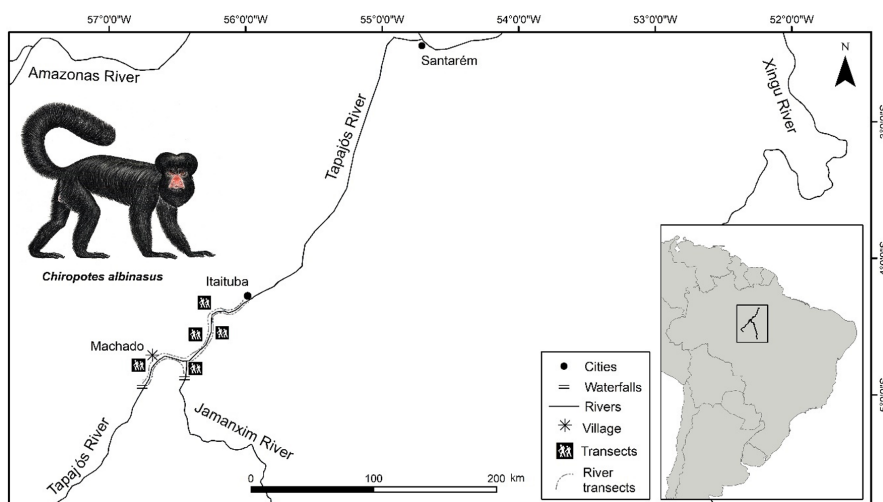
used the word “ort” for such material, a word defined as “a fragment of food, fallen from a table. A meal remnant” (<https://www.merriam-webster.com/dictionary/ort>). This usage was followed by Ballantyne (2018) and dos Santos-Barnett et al. (2022), and we use it here.

While monkeys can be messy eaters (Zagt, 1997), they are also often highly selective feeders (Chapman et al., 2012; Clink et al., 2017). Consequently, many previous studies have used ort-based methods to study diet composition and patterns of selectivity (Table S1). Thus, while an imperfect measure of dietary “selectivity” that requires controlled laboratory experiments for supportive verification, dropped fruit is often an important source of information in studies of wild primates.

The feeding remnant orts collected from beneath feeding trees are likely to be mixed with fruits handled and dropped without opening, and those opened and discarded without consumption. However, preliminary studies indicated that, for all sampled species, fallen whole fruits had the same proportions of infested/non-infested fruits on the ground as in the trees. It therefore appeared that cuxiús did not pluck then reject infested material, and that such fruits had simply been knocked down accidentally by movement. Accordingly, such material was not used in analysis, which focused purely on material that had been fed upon.

### 2.2.3 | Sample collection

Fed-at trees were flagged with marking tape. Any repeat visits by *C. albinasus* to individual trees were treated as independent events. Trees with very recent feeding signs (orts that were not discolored and/or still oozing sap or latex and bearing dental marks characteristic of *Chiropotes* feeding) were also sampled (see Figure 2). We did not collect orts or seeds that, based on discoloration or loss of texture, were considered likely to have been on the ground for longer than 1–2 h, since the action of foraging ants could have reduced insect content of such material greatly, and so bias results.



**FIGURE 1** Map illustrating the location of the study area and positions of land and water transects.



## 2.2.4 | Defining and collecting insect-infected fruits

Members of the genus *Chiropotes* have diets dominated by immature seeds from hard-husked fruits (Pinto et al., 2018). In such fruits, the husk, in addition to a low water content, is often rich in tannins and highly sclerified or fibrous (Cunha Junior et al., 2020; van Roosmalen, 1985), which may account for low frequency of their infestation by insects, compared to pulp or seeds (AA Barnett, unpublished data). However, pulpy fruits accounted for nearly half the species eaten (51 of the 117 species reported for the *C. albinasus* diet by Pinto, 2008). Consequently, both seeds and pulp (if present) were checked for the presence of resident infesting insects. We distinguished these from visiting scavengers by their presence in excavated tunnels, presence of frass, and individuals being at the larval (rather than adult) development stage.

To compare infestation levels, we analyzed values from fallen fruits (orts) with feeding marks and those from fruits on branches trimmed from trees *C. albinasus* had been observed to feed. To expand the sample, and more accurately assay the potential range of infestation levels, we collected fruit from the canopies of other individual trees belonging to known food tree species, but in which feeding had not been observed. All such trees were within 250 m of a tree in which *C. albinasus* had been observed feeding.

## 2.2.5 | Determining which primate species had deposited the collected orts

The two pitheciin species in the region (*C. albinasus* and *Pithecia mittermeieri*) leave different dental marks on orts than the other large-bodied primates of the central Tapajós (*Ateles chamek*, *Ateles marginatus*, *Alouatta discolor*, *Alouatta nigerrima*, *Cebus albifrons*, and *Sapajus apella*: de Oliveira et al., 2016), an effect of the marked differences in dental morphology and means of food processing of each taxon (Rosenberger, 2020). As pitheciins, *C. albinasus* and *P. mittermeieri*, have a unique feeding method (termed “sclerocarpic foraging” by Kinzey (1992)), which uses hypertrophied canines to penetrate fruit husks and procumbent incisors to extract seeds imparting characteristic dental impressions (see Figure 2) on fruit husks and any associated pulp. *Pithecia mittermeieri* was rarely seen and is smaller in body mass than *C. albinasus*, making it unlikely that orts from the two species would be assigned erroneously.

## 2.2.6 | Determining larval gut passage survivorship

To assess gut passage survivorship of larvae, we actively searched feeding areas for fecal pellets. *Chiropotes* pellets have a characteristic shape and form, resembling a large coffee bean, that allows them to be easily distinguished from those of similar-sized regional primates. The lack of sections of fiber and leaf fragments sets them apart from deer.

During sampling, fruit and seeds were stored in plastic zip-lock bags and labeled either as orts, fallen-uneaten fruits, or fruits removed from the tree. We stored fecal material in crush-resistant vials. All fruits, seeds, and fecal pellets were analyzed in a field lab within 3 h of collection and then preserved in alcohol.

## 2.2.7 | Plant species identification

Plants were identified to lowest possible taxonomic category using Gentry (1993), Ribeiro et al. (1999), van Roosmalen (1985), Neotropical Flora volumes (e.g., Mori & Prance, 1990), specialist literature (e.g., Procópio & Secco, 2008 for *Couratari*), and Harris and Harris (2001) and Jackson (2004) for botanical terminology. Identifications were confirmed using species lists in Pinto (2008: *terra firme*), Ferreira & Prance (1998: *igapó*), and comparison of photographs of fruits, seeds, leaves, flowers (when available), bark, whole tree (when possible) with on-line herbarium resources: Neotropical Herbarium Specimens, New York Botanic Garden, Tropicos, and Flore de Guyane (<https://www.fieldmuseum.org/node/4781>; <http://sweetgum.nybg.org/science/vh/>; <https://www.tropicos.org/home>, <https://floredeguyane.piwigo.com>, respectively).

## 2.3 | Data analysis

To test Prediction i (that a high percentage of the fruits eaten by *C. albinasus* would be infested by insects), the presence/absence of infestation was determined for the seeds in each individual fruit, and percentages were then calculated per plant species. This was done by analyzing orts discarded by *C. albinasus* and retrieved from the ground. Infestation intensity (measured as number of larvae or their total weight) was not quantified due to equipment failure.

To establish on-tree levels of infestation (key for Prediction ii, that foraging *C. albinasus* would select such infested fruits at a frequency disproportionate to their availability), fruits/seeds were sectioned, and the presence of insect larvae and/or damage associated with them (tunnels, bore-holes, frass, and discoloration) was noted. For each species, infestation was quantified using only fruits at the same maturation level as those eaten by *C. albinasus*. Following Barnett, Ronchi-Teles, et al. (2017); Barnett, Silla, et al. (2017) and Felton et al. (2008), we tested for selectivity of insect-infected fruit (Prediction ii) obtain from tree canopies using Electivity Indices (Ivlev, 1961) for each fruit species, such that:

$$(O_i - T_i) / (O_i + T_i)$$

where  $O_i$  = percent of orts with insect-infestation, and  $T_i$  = percent of on-tree fruit insect-infestation. Electivity values range from  $-1$  to  $+1$ , where  $+1$  indicates complete selection,  $-1$  indicates complete avoidance, and  $0$  indicates no preference (larvae-infested fruits selected at ambient value).



**FIGURE 2** A Sapotaceae fruit eaten by *Chiropotes*, showing the curved insertion point of the dental arc of the procumbent incisors, and the lateral rips subsequently made by the robust, splayed, and canines. Photo Credit: Justin A. Ledogar of fruit bitten by *Chiropotes sagulatus* in Suriname.

To provide comparability, and to ensure selection estimates were conservative, we used the same categories as Barnett, Ronchi-Teles, et al. (2017); Barnett, Silla, et al. (2017); values  $\pm 0.33$  to either side of zero (neutral) indicated no selection had occurred; values  $< -0.33$  indicated negative selection (active avoidance), and values  $> +0.33$  indicated active selection.

To assess whether fruit-infesting larvae passed intact and alive through the *C. albinasus* digestive system (Prediction iii), fecal pellets were broken apart with a thin glass rod. Material was then washed, sorted, placed in a petri dish, and scrutinized with a 10x hand-lens. We paid particular attention to the presence of invertebrate fragments, intact insect larvae, and pupae (the latter because they may not have been masticated due to small size). Any apparently intact individuals were prodded with a seeker tip to test for vitality.

To determine whether the force needed to penetrate the covering of the part eaten by *C. albinasus* is less for infested fruits than those whose non-infested status has left their pericarps intact (Prediction iv), we tested relative penetrability of the eight species with hard-husked indehiscent fruit (*Couratari stellata*, *Couratari cf. tenuicarpa*, *Eschweilera alba*, *Eschweilera obversa*, *Hevea spruceana*, *Lecythis lurida*, *Mabea nitida*, *Macrolobium acaciifolium*), and two species with hard, but indehiscent, fruit (*Chaunochiton loranthoides* and *Ternstroemia candolleana*). We used only hard-husked fruits, due to the differences in materials failure in brittle (dry shell) and ductile (pericarp-covered pulp) substances: in the former, cracks auto-propagate from the point of impact (Mode I fracture: cracking), while in the latter, propagation requires the application of continuous force (Mode III fracture: tearing or ripping) (Sun & Jin, 2012). Thus, just as a bored hole creates a zone of weakness in a rigid structure (Bao & Wierzbicki, 2004; Murdani et al., 2008), a bite is only

likely to facilitate post-canine insertion crack propagations in hard, non-elastic, husks, and not pulpy ones.

Like *C. ouakary* (Barnett et al., 2016), *C. albinasus* opens hard-husked fruits by biting selectively at areas of natural weakness (sutures of dehiscent fruit) or thinness (indehiscent fruit) (A.A. Barnett, unpublished data). Accordingly, following Barnett et al. (2015), Barnett, Ronchi-Teles, et al. (2017); Barnett, Silla, et al. (2017) we measured penetrability values at sutures and on between-suture faces using an International Ripening Company (Norfolk, VA 23502-2095) FT-011 fruit penetrometer, mounted on a replica Fridley Fruit Tester (Fridley, 1966), with the prosthetic cast of an adult female *C. albinasus* canine replacing the standard plunger head. Single measurements at, and between, sutures were made, to avoid the possibility of induced mechanical weakness induced by experimentally made holes affecting the values of subsequent measurements. We measured the force required not just to penetrate the husk, but also to reach the seed since some species (e.g., *Hevea spruceana*) have a second, inner, layer (the endocarp) harder than the outer epicarp (Muzik, 1954). Differences in penetrability were tested by comparing single measurements from the sutures and the areas between them for 10 infested and 10 uninfested fruits of each species (i.e., fruits with and without insect bore/oviposition holes using a Mann-Whitney *U* test). To avoid compromising the very structural integrity under investigation, all tested fruits were opened only after use, and the presence of infesting animals then ascertained. Level of significance was set at 0.05.

Although fungal infections have been shown to influence vertebrate choice of fruits, either positively (Buchholz & Levey, 1990) or negatively (Cipollini & Stiles, 1993), we did not investigate this variable, and excluded fruits with fungal rot from the data sets of all investigated species.

### 3 | RESULTS

A total of 4649 fruits from 130 trees or vines, representing 37 species in 30 genera and 18 families were analyzed. A total of 3249 fruits from trees were sampled, and 1400 fruits were sampled as orts. Of the 130 trees or vines from which fruits were obtained, 56 were sampled as a result of direct observation, while collections from 74 others represented sites where feeding had occurred very recently (e.g., fruit not discolored, and/or covered in ants; Table 1).

Of the 37 species recorded as eaten by *C. albinasus*, eight were exploited when both immature and mature (*Malouetia flavescens*; *Tabernaemontana* sp. – both Apocynaceae; *Dalium* sp., *Swartzia polyphylla* – both Fabaceae; *Couratari cf. tenuicarpa*, Lecythidaceae; *Calytranthus* sp., *Eugenia* sp. – both Myrtaceae; *Duroia* sp., Rubiaceae), providing a total of 45 diet items, with either the same part being eaten in both stages (seed: *M. flavescens*, *Tabernaemontana* sp., *C. cf. tenuicarpa*) or different parts of the fruit (e.g. whole immature pod vs aril in mature pod: *Swartzia polyphylla*: Table 1). Only one (*Iryanthera sagotiana*, Myristicaceae) definitively lacked any obvious



insect infestation. Of the remaining 44 species, selectivity could be determined for 41. For the other three species, fruits were ingested in their entirety, leaving no orts for analysis. Of the 41, fruits with infested seeds were positively selected in 20 (48.8%). In 15 of the 41 species (36.6%), fruits with infested and uninfested seeds were eaten at parity. In 6 species (14.6%), fruits with infested seeds were eaten at less than parity, and so appear to have been avoided.

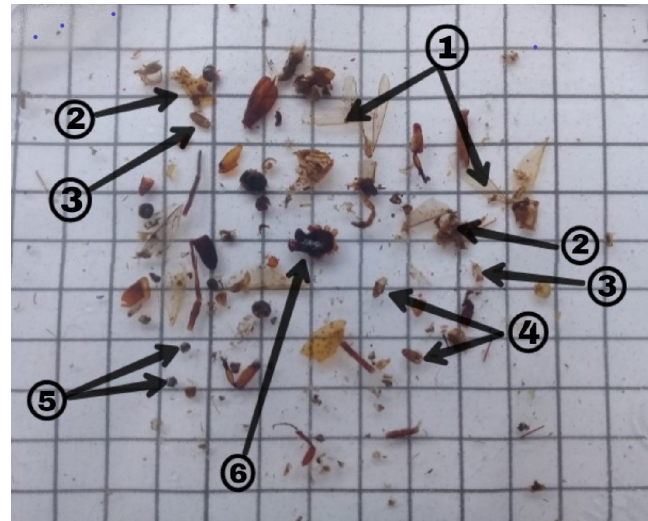
Thus, in terms of the overall diet, the incidence of infestation on by-species basis was high (44 of the 45 diet items analyzed: 97.8%), as were leveled for many species (Table 1). Additionally, within species, selectivity was relatively high with infested fruits being eaten at a greater frequency than parity for 26 species (63.4% of the 41 for which selectivity could be analyzed). Of these, 20 were positively selected (48.8% of analyzed species, and 76.9% of species for which selectivity was demonstrated: Table 1). Thus, Prediction i (that infestation would be high) is supported, and Prediction ii (that infested fruits would be eaten preferentially) is partially supported.

Analysis for living larvae and pupae was conducted on 13 *C. albinus* fecal pellets (Table 2). Of these, nine (69.2%) contained the remains of some form of invertebrate, most likely the result of *insectivory sensu stricto* (Ayres & Nessimian, 1982; Frazão, 1991; Pinto et al., 2018). There were, however, no living larvae and few larval remains (Table 2), apart from head capsules and other well-sclerotized parts and some areas of dermis. Pupal remains were also found, but none were intact (Item 4, Figure 3). Thus, Prediction iii is validated: neither insect larvae, nor pupae, survived passage through the gut of *C. albinus*. We did not record any intestinal parasites that might have been mistaken for seed-inhabiting larvae that had survived passage through the alimentary canal.

Comparative penetrability data for sutures and faces of fruits that were and were not infested were obtained for 10 species: eight with hard-husked dehiscent fruits, and two hard-husked indehiscent species (Table 3). For six of the tested species (including the two indehiscent), there were no significant differences between the penetrability faces of infested and uninfested fruits (statistical results are in Table 3). We also found no significant difference between the force needed to penetrate sutures for infested and uninfested examples of any of the eight fruits with dehiscent morphologies (statistical results are in Table 3). Hence, Prediction iv is not validated, and infested fruits were not more easily penetrated than uninfested fruit.

## 4 | DISCUSSION

Infestation levels were high in the fruit tested since of the 45 items from 37 species of fruits seen to be consumed by the monkeys only one lacked evidence of infestation. Selectivity could be estimated for 41 of the 44 infested items, with selectivity data lacking for three which were eaten whole. Of the 41, six (15%) appeared to have been avoided when infested, while in 20 (49%) fruits with infested seeds



**FIGURE 3** Invertebrate remains from a fecal pellet of *Chiroptes albinus*, showing fragments of spiders, and adult insects, but no larval insects associated with fruit infestation or their pupal stages. 1 = termite wings, 2 = caterpillar skin, 3 = elytra of small beetles, 4 = empty Dipteran pupal cases, 5 = caterpillar head capsules, 6 = body of a spider. Each square is 0.5 × 0.5 cm. Photo Credit: Adrian A Barnett.

appeared to have been preferentially selected. Fruits of 15 species (36%) were eaten at parity. Furthermore, none of the fecal samples showed any evidence of living pupae or larvae.

We found no difference in the penetrability of the husk face or suture for any of the 10 species analyzed, indicating that infested fruit choice was based on insect presence, rather than relative ease of access. Larval infestation was restricted to seeds in all studied cases. This is likely due to the dry, fibrous, tannin-rich nature of the pericarp of the species investigated and means that the obtained penetrability values therefore reflected those of likely to be encountered by a foraging *C. albinus*.

Overall, Prediction i (a high percentage of the species eaten by *Chiroptes albinus* would have seeds infested by insects) was supported, while partial support was obtained for Prediction ii (within species, *C. albinus* would select infested fruits at a frequency disproportional to their availability). Additionally, support was found for Prediction iii (fruit-infesting larvae would not be found whole and alive in the feces of *C. albinus*), but not for Prediction iv (for any given species, the force needed to penetrate the protective covering of the part eaten by *C. albinus* would be greater for fruits with uninfested seeds than those where seeds were infested). The fact that there was no difference between penetration force values at the suture for any of the tested species is significant since, like *Cacajao ouakary* (Barnett et al., 2016), *C. albinus* selectively bites at the sutures when fruits possess them (AA Barnett & T. de Oliveira, unpublished data).

As noted above, infesting insects may occur in both the pulp or seeds of fruit. In the current study, 17 of the 37 species of fruits recorded in the diet had pulpy pericarp (45.9%: a value close to that recorded by Pinto (2008) in the same region, 43.6%). Of these, eight

**TABLE 3** Comparative penetrability ( $\text{kg}/\text{mm}^2$ ) of faces and sutures of hard-husked fruits with infested and uninfested seeds eaten by red-nosed cuxiú (*Chiropotes albinasus*) on the Rio Tapajós, Pará State, Brazil.

Species	Uninfested face: Mean $\pm$ SD (range) <sup>a</sup>	Infested face: Mean $\pm$ SD (range) <sup>a</sup>	Significance	Uninfested suture: Mean $\pm$ SD (range) <sup>a</sup>	Infested suture: Mean $\pm$ SD (range) <sup>a</sup>	Significant difference?
<i>Chaunochiton loranthoides</i>	2.09 $\pm$ 0.07 (2.0–2.1)	2.07 $\pm$ 0.05 (2.0–2.2)	No ( $U = 41.5$ ; $p = .52$ )	n/a <sup>b</sup>	n/a	n/a
<i>Couratari stellata</i>	9.68 $\pm$ 0.12 (9.4–9.8)	9.48 $\pm$ 0.21 (9.1–9.7)	Yes ( $U = 20.0$ ; $p = .020$ )	6.27 $\pm$ 0.32 (5.8–6.6)	6.28 $\pm$ 0.27 (5.9–6.7)	No ( $U = 48.5$ ; $p = .91$ )
<i>Couratari cf. tenuicarpa</i>	2.27 $\pm$ 0.16 (2.0–2.5)	1.89 $\pm$ 0.20 (1.5–2.2)	Yes ( $U = 5.0$ ; $p = .001$ )	1.70 $\pm$ 0.13 (1.5–1.9)	1.73 $\pm$ 0.11 (1.6–1.9)	No ( $U = 46.0$ ; $p = .75$ )
<i>Eschweilera albiflora</i>	4.74 $\pm$ 0.83 (3.3–5.8)	3.79 $\pm$ 0.95 (2.5–5.0)	No ( $U = 25.0$ ; $p = .058$ )	3.08 $\pm$ 0.33 (2.6–3.7)	3.06 $\pm$ 0.55 (2.3–3.7)	No ( $U = 48.0$ ; $p = .91$ )
<i>Eschweilera obversa</i>	5.77 $\pm$ 0.91 (4.3–7.2)	4.68 $\pm$ 0.83 (3.3–6.0)	Yes ( $U = 19.0$ ; $p = .019$ )	3.04 $\pm$ 0.55 (2.4–4.0)	3.03 $\pm$ 0.52 (2.5–3.9)	No ( $U = 50.0$ ; $p = 1.00$ )
<i>Hevea spruceana</i>	3.01 $\pm$ 0.73 (1.7–3.8)	3.00 $\pm$ 0.64 (1.8–3.7)	No ( $U = 49.0$ ; $p = .94$ )	1.75 $\pm$ 0.24 (1.3–2.1)	1.74 $\pm$ 0.22 (1.3–2.0)	No ( $U = 47.0$ ; $p = .82$ )
<i>Lecythis lurida</i>	5.64 $\pm$ 0.41 (5.0–6.3)	5.20 $\pm$ 0.56 (4.3–5.9)	No ( $U = 30.0$ ; $p = .13$ )	5.20 $\pm$ 0.30 (4.8–5.8)	5.21 $\pm$ 0.27 (4.9–5.6)	No ( $U = 47.5$ ; $p = .85$ )
<i>Mabea nitida</i>	2.79 $\pm$ 0.34 (2.1–3.3)	2.13 $\pm$ 0.47 (1.5–3.1)	Yes ( $U = 15.0$ ; $p = .008$ )	1.86 $\pm$ 0.26 (1.5–2.4)	1.89 $\pm$ 0.17 (1.7–2.2)	No ( $U = 43.5$ ; $p = .62$ )
<i>Macrobolium acacifolium</i>	3.03 $\pm$ 0.21 (2.7–3.4)	3.07 $\pm$ 0.29 (2.7–3.6)	No ( $U = 42.0$ ; $p = .54$ )	5.37 $\pm$ 0.39 (4.8–6.0)	5.35 $\pm$ 0.49 (4.8–6.2)	No ( $U = 48.5$ ; $p = .91$ )
<i>Ternstroemia candolleana</i>	1.84 $\pm$ 0.22 (1.5–2.2)	1.67 $\pm$ 0.31 (1.3–2.1)	No ( $U = 34.5$ ; $p = .24$ )	n/a <sup>b</sup>	n/a	n/a

<sup>a</sup>Sample size is 10.

<sup>b</sup>Indehiscent fruit.

had records of infestation in both the pericarp and seeds, while in nine only the seeds were infested (Table 1). No eaten fruit had only pulp infested.

Penetrometer values showed insect presence does not make it easier to open a hard-husked fruit. Furthermore, the insects ingested (we saw no evidence that they were spat out) appear to have been digested, since none appeared as living larvae or pupae in fecal samples. The lack of living insects in *C. albinasus* fecal samples contrasts with those of other neotropical seed eaters, where living larvae and pupae of fruit-infesting insects have been found (see Guix & Ruiz, 1995, 1997 for birds). Indeed, while diverse remnants of adults occurred in the analyzed *C. albinasus* fecal samples (see Table 3), larval material was represented by just a few head capsules (item 5 in Figure 3), setae and material resembling caterpillar skin (item 2 in Figure 3). This probably occurred because larvae are generally very lightly sclerotized, so that most parts would be unlikely to survive the digestive passage intact.

The variation recorded here in *C. albinasus* selectivity of fruit with infested seeds (i.e., select, parity, and reject) has also been reported for *C. ouakary* (Barnett et al., 2015) and *Ateles* spp. (dos Santos-Barnett et al., 2022). As with these species, experimentally verified explanations for this range of responses is lacking. However, cases where infested items are selected at parity may reflect some form of frequency-dependent selection, where the chance of encountering an item is sufficiently large that the extra time spent in active searching is not compensated for in enhanced returns. Meanwhile, cases where fruits with infested seeds are selected at parity may be due to avoidance of chemicals synthesized as part of the plant's defensive response to seed infestation, including those where plants selectively accumulate toxic compounds within such infested seeds (Ibanez et al., 2009), as well as insect countermeasures where larvae sequester such compounds for their own defense (Ferro et al., 2006).

Some responses by *C. albinasus* clearly showed fine adjustments in foraging techniques. For example, very young pods of *Swartzia polyphylla* (Fabaceae) were eaten in their entirety (as humans would eat petit pois), while in more mature fruits only the sarcotesta is eaten. By weight, the sarcotesta is a very small proportion of the entire seed (less than 5%), an aspect that might well have influenced the selectivity pattern observed. In species where infested seeds were generally avoided, a few were recorded as being eaten (e.g., *Inga*). However, under such circumstances, the missing (i.e., eaten) portions appeared not to have insect-bored galleries continuing into them. Given the lack of the kind of direct action by insects that would induce a phytochemical response, we consider it probable that such areas did not have higher levels of toxic chemicals than other parts of the seeds of conspecifics.

Infestation was common with 44 of the 45 food items (98%) having some individuals that were infested. Of the infested items, 20 (45%) were positively selected. We attribute this to the nutritional benefits of insect consumption. Although we have focused here on the potential benefits of larvae as supplements in an immature seed-dominated diet potentially deficient in protein (Bukkens, 1997), it should be noted that insect larvae can also function as sources

of minerals, amino acids, and vitamins (Drew, 1988; Finke, 2013). Indeed, accessing such supplements from insect larvae may be particularly efficient, since the generally low levels of sclerotization of larval exoskeletons results in their being more easily digested than those of imagoes (Hopkins & Kramer, 1992; Raubenheimer & Rothman, 2013). Furthermore, since infesting larvae are concentrated within the boundaries of the seed, they also represent a clustered resource whose exploitation is more time/energy efficient than the more spatially dispersed adults (Barnett et al., 2020; McNamara & Houston, 1987). This may be significant since, in some fruits, infesting insects can constitute up to 35% of the total mass (Barnett et al., 2022; Barnett, Ronchi-Teles, et al., 2017; Barnett, Silla, et al., 2017).

However, this foraging approach is not without risks since damaged seeds may contain aflatoxins, which are inimical to mammals (Janzen, 1977; Massey et al., 1995). Accordingly, the avoidance of some plant species may be a reflection of aflatoxin avoidance. In addition, such fruits may have already had a substantial proportion of their material consumed – potentially offsetting the energetic gains obtained from animal material ingestion (Muñoz & Bonal, 2008).

Thus, we have shown that while it is a species already known to eat large free-ranging adult insects (Ayres & Nessimian, 1982; Frazão, 1991; Mittermeier et al., 1983; Veiga & Ferrari, 2006), as well as large spiders and their egg sacs (Moura, 2016), *C. albinus* also appears to practice covert carnivory (sensu Barnett, Ronchi-Teles, et al., 2017; Barnett, Silla, et al., 2017), eating insects concealed within seeds, and appearing to actively select infested seeds when doing so.

*Chiropotes* is a pitheciin, a group of neotropical primates that are generally considered to be seed predators and thus a group whose dietary strategies work in opposition to the reproductive interests of the plant species on which they feed. However, since many of the plant species involved have fruiting periods long enough to support several sequential generations of seed-predating insects (e.g., multi-voltine species: Janzen, 1976), the apparent capacity of *C. albinus* (and presumably other members of the clade) to digest larvae, could act as a source of population control for such insects. This may be especially pertinent given that fruits with infected seeds are preferentially selected. Combined with observations that pitheciin species can also act as seed dispersers (Barnett et al., 2012), this underscores the fact that not all pitheciin intersections with plants in their diet are predatory.

Covert carnivory may also be underestimated in other plant forms. Other potential insect-rich sources include buds, developing flowers, and young shoots (dos Santos-Barnett unpublished data), while young, unopened, leaves may house concealed caterpillars (Barnett, de Oliveira, et al., 2018; Barnett, Todd, & de Oliveira, 2018). Many primates, including *Chiropotes* spp., are also known to eat buds (stem, leaf, and flower) and flowers (Boyle et al., 2012; Di Fiore et al., 2008; Felton et al., 2008; Gregory, 2011; Russo et al., 2005). Given the ubiquity of bud-borers (Hanover, 1975; Sugiura & Yamazaki, 2009), and the often extensive presence of larval insects in budding and open leaves (Liu et al., 2015), and flowers

(e.g., Barnett et al., 2020 for *Eschweilera tenuifolia*, Lecythidaceae), it is possible that covert carnivory occurs here too. Along with observing insectivory on 18 occasions over a year-long study of *Chiropotes sagulatus*, Gregory (2011) observed frequent (101 bouts) consumption of Lecythidaceae flowers, and found that most of the fallen flowers inspected on the ground were infested with a variety of insect larvae. Additionally, older *Pradosia caracasana* (Sapotaceae) fruit opened by *C. chiropotes* in Venezuela had (bruchid) beetle emergence holes (M Norconk, unpublished data).

Furthermore, while *Chiropotes* spp. are known to eat the succulent leaf-bases and central stems of epiphytes, this may not be a source of water, as commonly supposed for primates (Galetti & Pedroni, 1994; Peres, 2000; Wright, 2004). Instead, they may be consuming insects, since such areas are commonly colonized by Dryophthorid weevils of the genus *Metamasius* (Cave et al., 2006), which are bromeliad-tissue specialists and can reach high densities (Frank, 1999). Additionally, Pinto et al. (2018) reported 39 instances of leaf galls being eaten by *C. albinus* (though insect type was not identified). Galls can be important sources of insect-derived protein (Milton & Nessimian, 1984) and are known to be eaten by a range of other primates (e.g., indri lemur, *Indri*: Britt et al., 2002; patas monkey, *Erythrocebus patas*: Isbell, 1998; Hanuman langur, *Presbytis entellus*: Srivastava, 1991; chimpanzee, *Pan troglodytes*: Tutin & Fernandez, 1993; Rio Mayo titi, *Plecturocebus oenanthe*: Deluycker, 2012; Chamek spider monkey, *Ateles chamek*: Wallace, 2005). Thus, it is possible that such ingestion again serves as a supplemental source of insect-derived protein. In addition, Shaffer (2013) noted that *C. sagulatus* would eat adult beetles present within Fabaceae pods, but not in the seeds. Though this was observed in fieldwork for the current study and may represent a source of additional protein, beetle presence was not quantified. Given the large number of small beetle-like legs and small elytra that were present in the fecal pellets (item 3, Figure 3), it seems likely that such taxa also form part of the *C. albinus* diet.

Of the 37 species of fruits studied, 17 had a pulpy exterior, and in eight this area was also infested with insects. Thus, it is possible that they, rather than the insects in the seeds, alerted and attracted the foraging monkeys. Irrespective of this, the fact that covert carnivory occurs in *C. albinus* remains unaltered. Together, this and the information above support the original contention of Redford et al. (1984) who were the first to propose that primates might gain protein from eating larval insects in food items, but whose insight was widely overlooked until recently.

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#### CONFLICT OF INTEREST STATEMENT

No potential conflict of interest was reported by the authors.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fn2z34v0b> (Barnett et al., 2022).

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