Journal of Zoological Research
Volume 1, Issue 1, 2017, PP 16-31

Covert Carnivory? A Seed-Predating Primate, the Golden-Backed Uacari, Shows Preferences for Insect-Infested Fruits.

Barnett A A[1,2,3,4*], Ronchi-Teles B[2], Silva WS[5], Andrade R[6], Almeida T[7], Bezerra BM[8], Gonçalves de Lima M[9], Spironello WR[2,4], MacLarnon A[1], Ross C[1]& Shaw PJA[1]

[1]*School of Life Sciences, University of Roehampton, London, SW15 4JD, England.*

[2]*Núcleo de Biodiversidade Instituto Nacional de Pesquisas da Amazônia (INPA) Manaus, Brazil.*

[3]*Amazon Flood plain Research Group, INPA, Manaus, AM, 69067-375, Brazil.*

[4]*Amazon Mammals Research Group, INPA, Manaus, AM, 69067-375, Brazil.*

[5]*Instituto de Ciências Exatase Tecnologia, Universidade Federal do Amazonas, Itacoatiara, Brazil*

[6]*Departamento de Química, Universidade Federal do Amazonas, Manaus, AM, 69077-000, Brazil.*

[7]*Laboratório de Herpetologia, Universidade Federal do Matto Grosso, Boa Esperança, Brazil.*

[8]*Department de Zoologia, Universidade Federal de Pernambuco, Recife, PE, 50100-130, Brazil.*

[9]*Protected Areas Effectiveness Unit, Protected Areas Programme, United Nations Environment Program, World Conservation Monitoring Centre, 219 Huntingdon Road, Cambridge, England.*

***Corresponding Author:** Barnett A.A., School of Life Sciences, University of Roehampton, London, SW15 4JD, England.*

ABSTRACT

Insect ingestion is generally recorded when consumption of free-living mobile prey is observed. However, an infrequently-investigated alternative exists: ingestion of insects living within fruits and/or their seeds. Potentially this offers frugivorous vertebrates a substantial source of animal protein, vitamins and micronutrients. Here we report on selection by the golden-backed uacari, Cacajao ouakary, *of fruits for their insect content. A Neotropical primate specialized for eating unripeseeds of hard-husked fruits,* C. ouakary *ate seeds/fruit pulp of 101 plant species, of which 26 showed insect infestation. Comparison of frequencies of infestation in fruits/seeds in diet-fruit remnants with those for on-tree same-aged con specific fruits, showed uacaris were: selecting infested fruits (11 species), eating at uniform frequency (9 species), or actively avoiding (6 species). Infested fruit/seed selection was not based on mechanical advantage from fruit weakened by insect burrows, since* C. ouakary *preferentially bite pericarp sutures, into which larvae do not burrow. By number of feeding records, the 11 actively-selected plant species contributed >25% of uacaris diet, and the 26 larvae-infested species 41.3%; at least 10.7% of individual fruit uacaris ateare estimated to have been insect-infested. Larval content varied from 0.4-5.5g per fruit, so this form of insectivory may make a significant contribution to* C. ouakary *diet. As larvae are commonly 60-80% protein, infested-fruit selection may be an important means for primates to access protein not otherwise easily available from fruits/seeds. We consider this topic important for understanding primate foraging decisions, and suggest diet-sampling methodologies should consider this foraging mode. Methods for detecting seed predation could be employed, both within and outside primatology, to recalibrate the contribution of fruit-inhabiting insectsto diets of species considered predominantly frugivorous.*

Keywords: Cacajao, *insectivory, preferential infestation selection, primate, seed-predation;*

INTRODUCTION

Insects may make significant nutritional and energetic contributions to primate diets (Bryer *et al*., 2015). However, ingestion of free-ranging insects by primates has long been considered underestimated (Chivers, 1969), and insect ivory resulting from ingestion of infested fruits (and their seeds) even more so (Redford *et al.*, 1984). Even when ingestion of fruit/seed-inhabiting insects is reported, the significance of their origin is rarely commented upon (e.g. Sazima, 1989: Appendix ONE). Yet, from a purely nutritional perspective, infested seeds should be selected preferentially, since existing levels of plant protein (Kinzey & Norconk,1993; Norconk *et al.*, 2009) will be supplemented by those of the larvae (Table 1A,B). While such direct preferential selection and ingestion has been recorded for some bird (Scott & Black, 1981; Piper, 1986) and mammal (Silvius, 2002; Valburg, 1992a) species, there are also good reasons not to eat infested fruit (Table 2A), and records also exist of frugivores rejecting these (Table 2B).

Table1. *Factors Contributing to Elevated levels of protein and other Nutrients in infested seeds.*

Observation Type	Comment	References (noticed in text)
Elevated protein and nutrient levels in infested fruits	Whilst both seeds and other fruit parts naturally contain protein (Kinzey & Norconk, 1993), the concentrations are lower than the 60-80% of wet-weight recorded by Bukkens (1997) for insect larvae.	Bukkens, S.G.F. (1997). The nutritional value of edible insects. Ecol. Food Nutr. **36**, 287–319.
Relative ease of larval digestibility	Insect larvae, generally being more lightly sclerotized, are often easier to digest than imagos (Raubenheimer & Rothman, 2012).	Raubenheimer, D. & Rothman, J.M. (2013). Nutritional ecology of entomophagy in humans and other primates. Ann. Rev. Entomol. **58**, 141-160.
Relatively low levels of protein in ripe seeds	While seeds are generally the most protein-rich part of a fruit (Norconk *et al.*, 2009), protein levels are generally lower in unripe seeds (Hill & Briedenback, 1974).	Hill JE & Breidenbach, RW. (1974). Proteins of soybean seeds II. Accumulation of the major protein components during seed development and maturation. Plant Physiol. **53**, 747-751.

Table2A. *Reasons to avoid infested fruits.*

Observation type	Comment	References (notcited in text)
If infestation of fruit/ seed extensive, or large parts already ingested by larvae, energetic/nutritive values of infested fruits/seeds maybe lower than non-ingested ones	Infested fruits avoided by squirrels (*Sciures carolinensis*: Steele *et al.*, 1996) and mice (*Mus spretus*: Muñoz & Bonal, 2008)	Muñoz A. & Bonal R. **(**2008). Seed choice by rodents: learning or inheritance?. Behav. Ecol. Sociobiol.**62**, 913-922.
In a cache, larvae-bearing seeds may contaminate others,	Occurs with squirrelacorn caches (Steele *et al.*, 1996)	Cited in text
Infested fruit/seed could be poisonous as plants may respond to infestation with localized manufacture of toxins	Localized toxin production known to occur in some species (*Protasparagus*, Asparagaceae: Knight, 1987; *Psophocarpus*, Fabaceae: Gatehouse *et al.*, 1991; *Mimosa*, Fabaceae: Kestring *et al.*, 2009. For general reviews, see Tollrian & Harvell, 1999; Edwards & Singh, 2006),	Edwards, O. & Singh, K.B. (2006). Resistance to insect pests what do legumes have to offer? Euphytica **147**, 273-285; Gatehouse, A.M.R., Hoe, D.S., Flemming, J.E., Hilder, V.A., Gatehouse J.A. (1991). Biochemical basis of insect resistance in winged bean (*Psophocarpus tetragonolobus*) seeds. J. Sci. Food Ag. **55**, 63–74. Kestring D, Menezes LC, Tomaz CA, Lima GP, Rossi MN. 2009. Relationship among phenolic contents, seed predation, and physical seed traits in *Mimosa bimucronata* plants. J. Plant Biol.**52**, 569-576. Knight RS. 1987. Coping with seed parasitism: a possible response by *Protasparagus aethiopicus.* Oikos **48**, 15-22. Tollrian, R. & Harvell, C.D. (Eds.). (1999). The ecology and evolution of inducible defenses. Princeton University Press.
Damaged plants tissue may be come toxic via fungal infestion.	Damaged plant issue is often colonized rapidly by a range of Spoil age fungi known to synthesize toxic molecules, including aflatoxins and patulin, some of the most potent carcinogens known (Janzen, 1977).	Cited in text
Inimical chemical may be sequestered and concentrated by larvae, enhancing risks associated with in-fruit/seeding sect ivory	Chemical known to be inimical to primates known to be sequestered or synthesized with in insect larvae (e.g. Martin & Müller, 2007).	Martin, N. & Müller, C. (2007). Induction of plant responses by a sequestering insect: relationship of glucose inolate concentration and myrosinase activity. Basic App. Ecol. **8**, 13–25.

Table2B. *Example of Avoiding Infested Fruits.*

Observation	Reference
23% of Bunch berry (*Cornus canadensis*, Cornaceae) fruits infected by invertebrates, but only 2% of fruits removed by vertebrate frugivores were infested. A version considered due to changes in palatability – either induced chemical changes or waste product accumulation. Also true in Buchholtz & Levey (1990), Christensen & Whitham (1991), Manzur & Courtney (1984), Christensen & Whitham (991), Manzur & Courtney (1984), Stiles (1980).	Burger, A.E. (1987). Fruiting and frugivory of *Cornus canadensis*, in boreal forest in Newfoundland. Oikos **49**, 3-10. (Buchholtz & Levey, 1990, cited in text) Stiles, E.W. (1980). Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. Am. Nat. **116**, 670-688.
Clark's Nutcrackers (*Nucifraga columbiana*) avoid cones of Colorado Pinion Pine (*Pinus edulis,* Pinaceae) that are infested by larvae of the pinyon tip moth (*Dioryctria albovittella*, Pyralidae)	Christensen, K.M. & Whitham, T.G. (1991). Indirect herbivore mediation of avian seed dispersal in pinyon pine. Ecology **72**, 534-542.
Blue Jays (*Cyanocitta cristatus*) avoid acorns of the Pin Oak (*Quercus palustres*, Fagaceae) when infested with larvae of *Curculio* sp. weevils	Dixon, M.D., Johnson, W.C. & Adisson, C.S. (1997). Effects of weevil larvae on a corn use by blue jays. Oecologia **111**, 201-208.
Brown pigeon (*Macropygia phasianella*) selectively ate fruit of *Solanum mauritianum* (Solanaceae) infested with *Dacusca cuminatus* (Tephritidae), while rodents selectively consumed *D. halfordiae* larvae in fallen fruit of *Planchonella australis* (Sapotaceae)	Drew, R.A.I. (1987). Reduction in fruit-fly (Tephritidae, Dacinae) populations in their endemic rain-forest habitat by frugivorous vertebrates. Aust. J. Zool. **35**, 283-288.
Avian frugivores (Mistle Thrush, *Turdus viscosos*, and Ringouzel, *T. torquatus*, avoid fruits of Common Juniper (*Juniperus communes*, Cuprescaceae) when infested with a seed-predator Chalcid wasp (*Megastigmus bipunctatus* Torymidae) and/or a pulp-sucking scale insect (*Carulaspis juniperi*, Diaspididae)	García, D., Zamora, R., Gómez, J.M. & Hódar, J.A. (1999). Bird rejection of un healthy fruits reinforces the mutualism between juniper and its avian dispersers. Oikos **85**, 536-544.
Avian frugivores avoid fruits of American holly (*Ilex opaca*, Aquioliaceae) when infested by the holly berry midge (*Asphondylia ilicicola*, Cecidomyiidae) (note: insect not inimical: the larvae chemically prevent the berry turning red).	Krischik, V., McCloud, E.S. & Davidson, J.A. (1989). Selective avoidance by vertebrate frugivores of green holly berries infested with acecidomyiid fly (Diptera: Cecidomyiidae). Am. Midl. Nat. **121**, 350-354.
Blackbirds (Turdusmerula) avoid fruits of Hawthorn (*Crataegus monogyna*, Rosaceae) infested by larvae of the Hawthorn moth (*Blastodacna hellerella*, Parametriotidae)	Manzur, M.I. & Courtney, S.P. (1984). Influence of insect damage in fruits of hawthorn on bird for aging and seed dispersal. Oikos **43**, 265-270.
Varied Thrushes (*Ixoreus naevius*) and American Robins (*Turdus migratorius*) avoid fruits of Blue berry (*Vaccinium ovalifolium*, Ericaceae) that are infested by larvae of a sawfly (*Melastolares unicolor*, Tenth red inidae) or a moth (Cranberry Fruit worm, *Lotisma trigonana*, Copromorphidae)	Traveset, A., Willson, M.F. & Gaither Jr, J.C. (1995). Avoidance by birds of insect-infested fruits of *Vaccinium ovalifolium*. Oikos **73**, 381-386.
From West Indian Sage (*Lantana camera*, Verbenaceae) frugivores removed fewer fruits damaged by the seed mining fly *Ophiomyia lantanae* than undamaged fruits. Authors concluded this suggested that frugivores were selecting against damaged fruit.	Vivian-Smith, G., Gosper, C.R., Wilson, A. & Hoad, K. (2006). *Lantana camara* and the fruit-and seed-damaging fly *Ophiomyia lantanae* (Agromyzidae): Seed predator, recruitment promoter or dispersal disrupter?.Biol. Contr. **36**, 247-257.

However, where infested fruits/seeds do not have higher levels of toxins than uninfested ones, they could be preferentially selected as a convenient co-package of animal-and-plant-based nutrients and proteins (Silvius, 2002). Alternatively, as larval bore-holes and female oviposition holes (Toju *et al.*, 2011) might structurally weaken the pericarp of hard-husked fruit (Borowicz, 1988; Prasifka *et al.*, 2014), frugivores/graminivores such as primates might be choosing such fruits based on mechanical advantage rather than nutritive benefit, simply because they are easier to break open (Barnett, 2010). Here we present an investigation of the nature and extent of insect-infested fruit consumption by the golden-backed uacari (*Cacajao ouakary*: *sensu* Ferrari *et al.*, 2014: Fig. 1), a primate that lives primarily in *igapó*, a seasonally-flooded forest type in north-west Amazonia (Junk, 1997), and has an annual diet consisting of 80% unripe fruits and their seeds (Barnett *et al.*, 2013; Bezerra *et al.*, 2011).

Generally considered seed-predators (Kinzey & Norconk, 1993; Norconk *et al.*, 2009), uacaris (*Cacajao*) and their relatives (the cuxius, *Chiropotes*, and sakis, *Pithecia:* Pitheciinae, Pitheciidae) have diets containing high percentages (60-80%) of seeds derived from unripe fruit with hard pericarps (Norconk *et al*., 2013). Members of all three genera also eat ripe fruit, leaves and insects (Veiga & Ferrari, 2006; Barnett, Bowler *et al*., 2013; Norconk & Setz, 2013). Studies of pitheciine insectivory have focused on predation of free-ranging arthropods (e.g. Ayres & Nassimian, 1982; Mittermeier *et al*., 1983), even though they also eat fruits/ seeds containing insect larvae (Ayres, 1986).

Frugivorous vertebrates can cause substantial mortality to fruit- and seed-dwelling insects (Herrera, 1989; Peguero & Espelta, 2013). Many insect larvae feed only on pulp or seeds of unripe fruits, emerging just before these ripen (bruchid beetles: Southgate, 1979; pyralid moths: Dreyer, 1984; tephritid flies: Herrera, 1984); a possible avoidance strategy as most vertebrate frugivores eat ripe fruit (Sallabanks & Courtney, 1992). However, as pitheciins eat large quantities of seeds from unripe fruits, they might be expected to encounter such insects before their emergence. This, plus the fact that unripe fruits and their seeds are often low in fats and proteins (Norconk *et al*., 2009), could mean that uacaris might preferentially select insect larvae-infested fruits/seeds. Based on the null hypothesis that insect larvae presence in fruits/seeds insect will not influence the possibility of their selection by the golden-backed uacaris (either negatively or positively), we tested the following predictions:

- In infested fruits, larvae will not contribute significantly to the mass of seed(s);
- Within a plant species, uacaris will not preferentially select ingest infested fruits, therefore these will not be ingested at levels proportionally greater than their occurrence on parent trees;
- Fsor hard-pericarp fruit, pericarps of fruits infested with insects will not be easier to penetrate.

MATERIALS AND METHODS

Study Site

From Oct 2006-Jul 2008 we conducted field studies in Jaú National Park, Amazonas, Brazil, between Cachoeira do Jaú (01° 53.2"S, 61° 40.4"W) and Patuá village (01° 53.1"S, 61° 44.3"W) (Fig. 3). These sites are <15 km apart and have the same vegetation cover and climate. Studies occurred in never-flooded forest (*terra firme*) and *igapó* (seasonally-flooded river-margin forest).

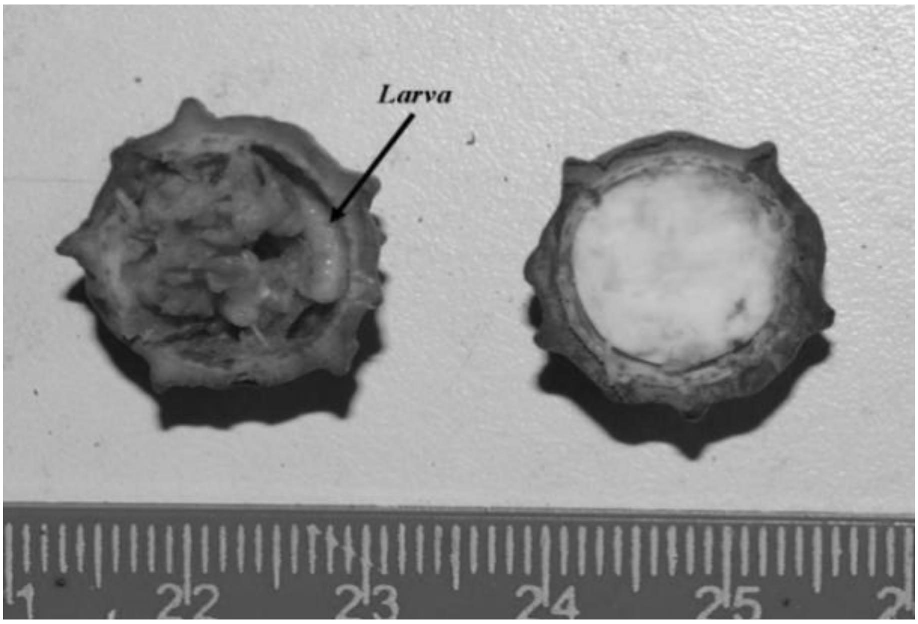

Figure1. *Fruits of Chaunochiton loranthoides (Olacaceae). Right uninfested fruit; left infested fruit with larve (arrowed) of Anestrepha sp. Nov. (Tephritidae).*

Field Protocols

Golden-backed uacaris were searched for on foot in terra firme, and from paddled canoes in flooded igapó. When encountered, behaviour was recorded with instantaneous scan sampling, with intervals of five-minutes (Altmann, 1974). Data categories were: foraging, moving, resting, social (Barnett, 2010). Following Ferrari (1988), we used supplemental *ad libitum* sampling to gain additional foraging behavior details (see Appendix TWO for details of behavior recording methodology, plus Barnett *et al*., 2013, 2015, 2016). Primate feeding generally results in debris (orts), analysis of which can provide insights into feeding processes and diet choice (Burger, 1987; Forget *et al.,* 1994). Using such material in this manner has a strong canonical history in ecology (e.g. Tutin *et al.* 1996, plus Appendix ONE). Consequently, diet samples were collected, immediately after uacaris left a tree, and all fallen fruit fragments (hereafter ´ort-fruits´) resulting from that feeding bout collected for analysis (see Appendix THREE for additional information). Infested fruits were recognized by the on-pericarp presence of: entrance bores and/or exit holes, discoloration, frass or cocoons. Plants were identified using Gentry (1993), Ribeiro *et al.* (1999), and field-collected material subsequently compared with exsiccates in the Instituto National de Pesquisas da Amazônia (INPA) Herbarium. Larval stage insects are often difficult to identify. Consequently, tree-collected infested fruit were keptat INPA-Entomology, emerging imagoes retrieved, and specimens identified by INPA entomologists and other researchers (see Acknowledgements).

We calculated the contribution of insect larvae to fruit mass, for five of the 26 tree species with insect-infested fruits in the golden-backed uacaris diet. These were: *Calyptranthes* c.f. *creba, Myrtaceae; Chaunochiton loranthoides*, Olacaceae*; Eschweilera tenuifolia,* Lecythidaceae*; Macrolobium acaciifolium*, Fabaceae*; Sloanea* sp., Elaeocarpaceae).

The species were chosen because they represented a range of morphologies and sizes. Fruits were searched for insects with the naked eye, then a10x hand lens. If fruits had pulp, this was progressively removed and seed(s) broken open. For dry fruits, pericarps were broken into fragments and seeds searched as above. For each species, masses of entire fruits and entire seeds were taken and re-measured following inhabiting insect removal. We weighed fruits exceeding 2g with Pesola spring balances and smaller fruits with a Salter electronic balance, in each case to 0.1g. For spherical fruits we measured diameter, for other shaped fruits we measured greatest length, in each case to 0.1mm with SPI 2000 dial calipers.

For all 26 species, we collected fruit used for calculating infestation rates from trees within 24 hours of uacaris feeding observations being made there. We assayed infested fruit selection for each by randomly selecting from the canopies fruits of the same maturation stage as those the uacaris had eaten. To avoid unconscious selection bias, we analyzed every third fruit of the appropriate developmental stage encountered on the sampled tree. Further details of fruit acquisition are given in Appendix THREE.

For fruit to be selected for insect content, consumed and infested parts (seed, pulp or seed + pulp) must be the same. Consequently, we recorded eaten and infested part(s) for all fruits golden-backed uacaris ate. On-tree fruit were considered infested if insect larvae or their spoor (tunnels, faeces) were detected in the same part that uacaris ate when feeding on conspecific fruits.

Although fungal infections have been shown to influence vertebrate choice of fruits (positively [Buchholtz & Levey, 1990], or negatively [Cipollini & Stiles, 1993]), this variable was not investigated; we excluded fruits with fungal-rot.

We did not observe fruits of any investigated species being ingested whole, and normal primate messy feeding behavior provided orts for analysis. The methods we used to avoid overestimation of infested-fruit/seed preference are given in Table 3.

Table3. *Methods Used to Avoid Overestimation of Infested-Fruit Preference*

Method	Rationale
Considered only ort-fruits that retained 50%, or more, of their original form.	Avoid the over-counting that could result if many small fragments counted as one individual diet item
Jig-sawing large fragments in case a fruit had simply been bitten but not eaten,	Attempt store construct whole fruits from existing large fragments was again an attempt to avoid over estimation of the number of eaten fruits
Include in the class ‘eaten-while-infested’ only fruits/ seeds where larval tunnels crossed the bite-mark surface (and the larval was not in the in-hand fruit section).	In theory larval tunnels (and larvae they contain) could all be in theory part of the fruit (running parallel to the bit surface, for example) and none occur in the eaten part. This method minimized this possibility.

We considered that uacaris had actively selected infested fruits/seeds when on-tree fruit infestation rates exceeded that in the ort-fruit debris. By the same logic, when the two ratios were equal (± 5%) there was no selection, while on-tree infestation rates less than those in ort-fruit debris indicated active selection of non-infested seeds (infested seed avoidance). When sampling debris under a tree in which golden-backed uacaris had been seen feeding, we collected only just-fallen ort-fruit (indicated by such features as still-oozing sap), and rejected any showing age-related discoloration, so minimizing dataset bias from fish feeding on fallen material (Waldhoff *et al.*, 1996). To avoid any re sampling errors, all ort-fruits and other feeding debris was completely removed from beneath any tree investigated.

Foraging golden-backed uacaris remove individual legume seeds from their pod compartments (Barnett, 2010). Such behaviour, plus compartments with infested seeds having discolored walls and/or containg frass (Kamel, 1982), allowed within-fruit selectivity of individual infested/non-infested seeds to be tested for pods of *Inga obidensis* and *I. rhynchocalyx*. We examined seed chambers on all collected pods, scoring as infected/non-infected, based on presence/absence of frass, discoloration or clearly infected seed(s).

To test relative penetrability of fruits with and without insect bore/oviposition holes, we selected five species (*Amanoa oblongifolia; Diospyros cavalcante; Eschweilera tenuifolia; Mabea nítida; Macrolobium acaciifolium*) which were dehiscent and possessed sutures. Following Barnett *et al.* (2015), 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, 1955), with the prosthetic cast of an adult female uacari canine replacing the standard plunger head.

Statistical Tests and Analyses

To examine if golden-backed uacaris were actively selecting infested or non-infested seeds, we used a two-way chi-square to test for significant differences in infestation levels between on-tree fruits and those of ort-fruit. Results are given in Table 4. Small sample size effects are indicated, as values of $N \leq 5$ make a two-way chi-square unreliable (Siegel, 1956). A chi-square test show whether there is a difference in fruit selection, but cannot demonstrate whether selection or avoidance is occurring. Therefore, to test if uacaris were selecting/rejecting infested fruits, or consuming them at parity, we calculated Ivlev Elective Ratios (*E*) (Ivlev, 1961), using:

$$(r_i - p_i) / (r_i + p_i)$$

Where r_i=percent of insect-infestion in ort-fruits, and p_i=percent of insect-infested in on-tree fruits at the same maturation level as those eaten by uacaris. *E* values range from -1 to +1 (with -1 indicating complete avoidance, 0 indicating no preference, and +1 indicating complete selection). To ensure all categories were of equal size (and so provide the most conservative selection estimate), cut-off points for null-selection were set at +0.3 to -0.3, with selection being considered active when values > +0.33, and values > -0.33 indicating negative selection (active avoidance).

We used Mann-Whitney U tests to examine whether significant differences existed between pericarp penetrability of conspecific fruits with/without insect bore/oviposition holes.

RESULTS

In 21 months we recorded golden-backed uacaris eating seeds of 101 plant species. Of these, 26 (25.7%) had insect larvae-infested seeds (Fig. 2), with rates varying from 8-80% (mean 25.82 SD±17.4: Table 4). Together, the 26 species represented 40.8% (4,860) of the 11,902 plant material feeding records. All 26 bore the characteristic marks of uacari teeth (see Appendix TWO), had seed(s) bitten through, and were observed being bitten by golden-backed uacaris during field work. In addition, we calculated larval mass as a percentage of total seed mass for five species: four single seeded (Table 4), and one multi-seeded species (see below).

For multi-seeded *Eschweilera tenuifolia*, of the 86 immature pyxidia from which uacaris ate seeds, 39 (45.3%) had live larval insects or seeds with larval insect damage. Of 50 immature pyxidia removed directly from *E. tenuifolia* trees, four (8%) were infested with insects. Of the 119 seeds from the four infested pyxidia, 106 (89.1%) were infested (70.5-100% per pyxidium). Larvae constituted a mean of 13% of infested fruit mass (range 7.5-27.5%). Commonest infesting insects were larvae of an unidentified clear-wing moth (family Sesiidea), and of an unidentified micro-hymenopteran. Small beetle larvae were also present.

Table4. *Absolute and the Mean Masses of Insect Larvae Infesting Seeds of Single Seeded Uacari Diet Fruits (fruits taken from trees)*

Species	N	N infested	% infested	N Larvae per infested Fruit, Mean (Range)	Absolute Mass (g) of Larvae per Fruit: Mean (Range)SD	Larval Mass as percentage of Fruit Total Mass, (Range)SD	Taxa infesting
Calyptranthes cf. *creba*	24	9	37.5	1.3 (1 - 3)	0.85(0.2 -1.4) ±0.48	44.20(25.0–61.1) ±11.44	Coleoptera larvae
Chaunochiton lauranthoides	48	11	22.9	4.2 (2 - 8)	0.97(0.4 - 2.1) ±0.61	53.70 (30.0–86.7) ±17.76	Larvae of *Anastrepha* sp. nov. (Tephritidae, Diptera)
Macrolobium acaciifolium	50	14	22	1.2 (1 - 2)	3.70 (1.2 - 5.5) ±1.50	39.70 (17.1–51.0) ±11.82	Coleoptera larvae
Sloanea sp.	11	3	27.3	2	3.28 (2.7 – 3.8) ±0.47	19.4 (16.0-23.2) ±3.6	Coleoptera larvae and adults
Mean values (SD)		**--**	**27.4 ±07.1**	**2.2±1.4**	**2.2±1.5**	**39.25±14.46**	--

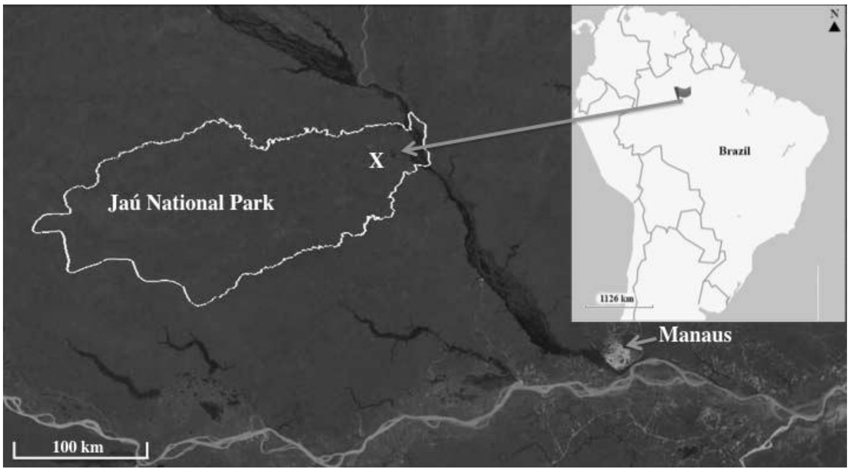

Figure2. *Map showing the location of Jau National Park in Brazil (insert) and the study site within the National Park (main frame).*

Parts eaten and parts infested.

For all 26 species, infestation occurred in the fruits/seed part eaten by golden-backed uacaris (Appendix FOUR).

Selection of Infested Fruits

Golden-backed uacaris positively selected fruits with insect-containing seeds (hereafter referred to as 'infested fruits' or a variant)for 11 of the 26 species (42%), ate infested fruits at parity with their on-tree frequencies in nine species (34.6%), and actively avoided infested fruits or seeds in 6 species (23.1%) (Table 5).

For two of eleven cases where golden-backed uacaris positively selected infested fruits, sample size of eaten fruit was too small (<12) for statistical analysis, leaving nine species (34.6% of infested diet species, and 8.9% of all 101 species eaten for seeds/pulp) for which positive selection can be statistically validated. Two species with Ivlev values indicating negative selection also had samples too small for statistical analysis (Table 5).

Apparent null-selection in some species may be a methodological artifact: multi-seeded pods of two *Inga* species were eaten whether they contained infected seeds or not (null selection), but individual infected seeds were almost always ignored (avoidance). Because insect infestation discolours pod walls and/or leaves frass, we could quantify this avoidance. Combined, the sampled 81 *Inga* spp. pods contained 641 individual seeds. While 167 were infested, only 7 (4.2%) showed signs of having been investigated (compartments opened) or eaten, compared with 84.4% (n=400) of un infested seeds. The difference is statistically significant (χ^2 = 125.129, *p*=< 0.0001) and indicates avoidance of infested seeds.

Differential Resistance of Pericarp – with and without Insect Bore Holes

Of the 26 species, seven had tough outer pericarps that, as they were either leathery or brittle, could have their resistance compromised by holes bored by larval/adult insects. We analysed five, and found bore/ oviposition holes presence made no significant difference to fruit-face penetrability in three species (*Diospyros cavalcantei, Eschweilera tenuifolia, Macrolobium acaciifolium*), and it did not affect penetrability at the sutures for any of the analysed five (Table 6). For the two species for which bore/ oviposition hole presence influenced fruit-face penetrability (*Amanoa oblongifolia*, *Mabea nitida*) uacaris bit on exclusively on-suture (uacaris generally bite dehiscent fruit at the sutures: Barnett *et al.*, 2016).

Table5. *Comparative frequency of Infested fruits on trees and in feeding debris.*

Species	**Fruits On Trees**			**Fruits In Feeding Debris**			**X^2 (Df=1) Test Value; P Value** Significant Values Are In Bold; Italics And Sss Indicate E Values <5	**Ivlev Electivoty Index Value** Selection Types P=Positive (Infested Selected); N=Negative (Infested Avoided); O=Null(No selection: -0.25 - 0.25); (Sss=Small sample Size)
	N	**N infested†**	**% infested**	**N**	**N infested†**	**% infested**		
Amanoa oblongifolia	50	32	64	26	0	0	**28.7<0.005**	-1.0, N
Bombacopsis macrocalyx	25	5	20	25	8	32	0.9NS	0.23, O
Calophyllum brasiliense	50	4	8	6	0	0	0.5 (SSS)	-1.0, N (SSS)
Calyptranthes c.f. *creba*	28	4	14.3	20	12	60	**10.9 <0.005**	0.62, P
Chaunochiton loranthoides	48	11	22.9	76	35	46.1	**7.0 <0.01**	0.34, P
Diospyros cavalcante	50	4	8	35	10	28.6	**6.3 <0.01**	0.63, P
Duguetia sp.	10	8	80	5	2	40	2.4 (SSS)	-0.33, N (SSS)
Duroia aquatica	30	7	23.3	7	2	28.6	0.8 (SSS)	0.10 O (SSS)
Duroia velutina	35	12	34.3	45	17	37.8	0.1 NS	0.05 O,
Elaeoluma glabrescens	35	3	8.6	50	18	32	**8.3<0.005**	0.58, P
Eschweilera tenuifolia	50	4	8	86	39	45.3	**20.4 <0.005**	0.86, P
Eugenia sp.	10	4	40	25	19	76	**4.1 <0.05**	0.31, P
Inga obidensis	50	9	18	45	10	22.2	0.3NS	0.10, O
Inga rhynchocalyx	50	14	28	6	2	33.3	0.7 (SSS).	0.09, O (SSS)
Licania heteromorpha	30	10	33	25	18	72	**8.2 <0.005**	0.37, P
Mabea nitida	50	27	52	30	0	0	**24.4 <0.005**	-1, N
Macrolobium acaciifolium	50	14	22	52	3	5.7	**9.1 <0.005**	-0.59, N
Mouriri guianesis	38	7	18.4	37	24	64.9	**16.7 <0.005**	0.65, P
Myrcia sp.	60	20	33.3	30	25	83.3	**6.7 <0.01**	0.43, P
Panopsis rubescens	50	6	12	50	6	12	0	0.0 O
Parkia discolor	50	10	20	11	1	9.1	0.7 (SSS)	0.41 ,P (SSS)
Protium sp.	10	2	20	4	0	0	0.9(SSS)	-1 N, (SSS)
Pouteria elegans	50	11	22	50	17	34	1.8 NS	0.21, O
Pouteria sp.	50	9	18	37	4	10.8	0.9 NS	-0.25, O
Sloanea sp.	11	3	27.3	7	5	71.4	3.4 (SSS)	0.45, P (SSS)
Swartzia polyphylla	20	4	20	50	10	20	0	0 O
Mean values	--	8.62 SD±7.2	25.82 SD±17.4	32.32 SD± 21.74	11.04 SD±10.92	33.27 SD±25.65		

Table6. *Comparative penetrability of sutures and faces of infested and non-infested fruits.*

SPECIES	***Uninfested Face (N=10) mean value (SD, range)***	***Infested Face (N=10) mean value (SD, range)***	***Stat. Signif diff. Face/Face***	***Uninfested Suture (N=10) mean value (SD, range)***	***Infested Suture (N=10) mean value (SD, range)***	***Stat. Signif diff. Sut./Sut.***
Amanoa oblongifolia	3.13 (±0.37, 2.6-3.6)	2.10 (±0.43,1.2-3.5)	z=3.1** YES	2.10 (±0.40,1.2-2.6)	2.30 (±0.40, 1.4-2.9)	z=1.1 NO
Diospyros cavalcante	3.40 (±0.37, 2.7-3.8)	3.36 (±0.38,2.8-3.8)	z=0.34 NO	1.87 (±0.30,1.4-2.3)	1.89 (±0.42, 1.3-2.4)	z=0.19,NO
Eschweilera tenuifolia	5.15 (±0.46, 3.4-5.7)	3.034 (±0.48, 3.4-5.7)	z=0.76 NO	4.80 (±0.78,1.8-3.7)	4.70 (±0.67, 1.4-3.8)	z=0.30,NO
Mabea nítida	3.07 (±0.67, 1.7-3.8)	2.07 (±0.59, 1.4-3.1)	z=2.84** YES	2.10 (±0.50,1.6-3.0)	2.03 (±0.49, 1.4-2.9)	z=0.8,NO
Macrolobium acaciifolium	2.99 (±0.14, 2.7-3.2)	3.05 (±0.15, 2.8-3.3)	z=0.68 NO	5.48 (±0.44,4.8-6.2)	5.30 (±0.52, 4.5-6.0)	z=0.76,NO

DISCUSSION

Study results showed concordance with predictions in the following ways: Prediction 1 (*in infested fruits eaten by golden-backed uacaris, larvae not will contribute significantly to the mass of the seed)*: not supported for the five species tested, as larvae constitute a mean of 45.8% of seed mass for single-seeded species, and 13% for multi-seeded species. Prediction 2 (*within a plant species, golden-backed uacaris will not preferentially ingest infested fruits): not* supported for nine of the 19 species for which statistically-viable sample sizes were obtained (47.4%). Prediction 3 (*in hard-pericarp fruit, the pericarp will not be easier to penetrate in insect-infested fruits*): not supported for two of the five species tested at the face, but supported for all species at the suture.

Current study results were, at first glance, not clear-cut: with positive selection for infested fruit indicated for some species (e.g. *Calyptranthes* cf. *creba*, *Eschweilera tenuifolia*), while in others infested fruit were either eaten at parity (e.g. *Duroia velutina)*, or avoided (e.g. *Amanoa oblongifolium, Macrolobium acaciifolium).*

Additionally, some apparent null selection was complex: for the legumes *Inga obidensis* and *I. rhynchocalyx*, golden-backed uacaris left infested seeds in the pod, while extracting and eating un infested seeds from the same pod. A possible explanation is that infesting larvae produce chemical gramnivore repellents, or that seed chemistry changes as plants attempt to kill invading animals (Janzen, 1977; Schaller, 2008). Thus, infested seeds may have been toxic, while un-infested ones were not. This may also explain uacari avoidance of infested *Amanoa*, *Mabea* and *Macroblobium* seeds. Avoidance of infested fruits has also been recorded by Philippine fruit-bats (Utzurrum & Heideman, 1991), and *Alouatta seniculus* in French Guiana (Julliot, 1996), though in neither case was a mechanism proposed (see Table 2B for avian examples).

Consumption of insects in fruit is often assumed to be passive (e.g. Link, 2003), and, indeed, will be so in figs, whose pollination biology (Weiblen, 2002) guarantees ingestion of larval / adult fig-wasps (Hymenoptera: Chalcidoidea) (though this is rarely considered, even when fig ingestion is recorded: Bravo & Zunino 1998 being an exception). In other instances, active choice of infested fruits occurs. This might be because infested fruits can be nutritionally more rewarding, since larvae synthesize proteins and fat (Valburg, 1992*a*), are vitamin-rich (Semel & Anderson, 1988; Steele *et al.* 1996) and infestation can increase fruit-flesh amino acid content (Drew, 1988).

Fruits infested by insect larvae were found in 25.7% of fruit species eaten by uacaris. Such seeds can provide substantial volumes of animal tissue: larvae constituted a mean of 45.8% of seed mass for four single-seeded species, and 13% of the multi-seeded fruits of *E. tenuifolia*. The potential importance of this becomes apparent when the likely volume of larvae thus consumed is considered: *Eschweilera tenuifolia* ranks second in golden-backed uacaris immature seed feeding records (Barnett, 2010), and uacaris positively select insect-infested *Eschweilera* seeds. These are large (≥ 6.5 cm), frequently exceed 30 per fruit, with often plentiful infestations (≥80% of seeds per fruit). Insect larvae in *E. tenuifolia* seeds could therefore be an important protein source for golden-backed uacaris. Other infested species also rank high in the diet (Appendix FOUR); together, the nine species for which selection was demonstrated constitute 21.5% of the recorded uacaris diet, with the 26 larvae-infested species contributing 41.3% of this (Barnett, 2010). Since the overall mean infestation rate was 25.8%, this means that over 10% of the uacaris diet potentially consists of insect-infested fruits. The capacity for larvae-within-fruit to make a significant, but heretofore little-recognized, contribution to the protein balance and energy budget of golden-backed uacaris is therefore great.

Dietary importance to Neotropical primates of fruit-infesting insects has been considered by a number of authors (Appendix ONE), including Ayres (1986) who thought *C. c. calvus* might actively select insect-containing fruits, and reported infestation levels similar to those found here (≥37% of entire fruit wet mass, and ≥73% of seed mass). Ayres (1986, 1989) noted that many immature fruits become heavily infested with coleopteran larvae, including *Licania parviflora* (Chrysobalenaceae), a uacari food-fruit, where 29 / 80 immature fruit (36.3%) were infested. Correspondingly, fruits eaten by Black howler monkeys (*Alouatta caraya*) had mean larval weevil infestation rates of 78% (Bravo, 2012), and capuchin monkeys stones to selectively break open the hard fruits of *Syagrus* palms that are infested with weevil larvae (Rocha *et al*., 1998).

Searching for animal prey is often a time-intensive business, since the taxa most commonly involved (grasshoppers, small spiders, bugs: see Barnett *et al*., 2013) are often cryptic, consequently their successful capture may require an elaborate and complex hunting strategies (Schiel *et al*., 2010). The use of concealed prey to gain access to animal fat and protein may, therefore, be especially significant for time-limited species such as uacaris (Barnett, 2010) since, whilst energy must be expended in opening the material in which such animals are imbedded, this is offset by the certainty that there is an animal inside. Such security is not a feature when searching for free-ranging prey.

While the current study did not find positive selection of infested fruits in every instance, we have shown that such selection does occur. The ambivalence may occur because, while other studies often just treat one plant species (e.g. Bravo, 2012), we looked at several; other multi-species analysis found a similar spread of responses. For example, offered a choice of infested and non-infested fruits from seven diet species, Common Bush Finch-tanagers (*Chlorospingus ophthalmicus*, Emberizidae) preferentially consumed larvae-infested-fruits in four cases, rejected two, and ate fruits of one species at parity (Valburg 1992*b*).

Another possible variable is morphology; studied fruits represented several different types, including woody capsules (*Amanoa*, *Sloanea*), pyxidia (*Eschweilera*), near-pulp less drupes (*Diospyros*, *Chaunochiton*), and pulp-rich berries (*Duroia*, *Eugenia*). Cues that fruits are infested can be textural, visual or chemical (via either taste or volatiles) (Desouhant, 1998; Hern & Dorn, 2007); thus, given the different morphologies, species may have different maturation chemistries (Giovannoni, 2001; Rodríguez *et al*., 2013), and could respond quite differently to infestation *viz-a-vis* changes in coloration, hardness and odour. This could provide uacaris with a suite of differing cues regarding infestation, to which they may or may not respond with equal accuracy.

For insect-infestation preferences to result purely from mechanical advantage requires that pericarps will be easier to penetrate in insect-infested fruit. Yet for three of five hard-pericarp fruits investigated, penetration values between infested / non-infested fruits were not significantly different at either faces or sutures. It therefore seems unlikely that presence of bore/oviposition holes influences golden-backed uacaris selection of infested fruits; particularly since the only two species where bore/ oviposition holes made pericarp penetration easier (*Amanoa oblongifolia* and *Mabea nitida*) were rejected by uacaris when infested. Therefore, it appears plausible that golden-backed uacaris responses to infested fruits will be based more on chemistry and nutritional content than mechanical - physical considerations.

Positive selection for infested fruits has been shown for *Sciurus* squirrels (Steele *et al*., 1996), and *Peromyscus* mice (Semel & Anderson, 1988). But, despite a key review by Redford *et al*.(1984), the role of insect-infested fruits as a protein source in primate diets remains significantly under-researched (see Appendix ONE), and is clearly needs further quantitative study. However, while the true extent of this method of gaining protein remains to be assessed, it may be widespread - certainly consumption of galls (structurally similar to infested fruits and likely to have 100% insect occupancy) is known for many primate taxa (Appendix FIVE). When insectivory studies begin to include species concealed within fruit, revealed levels of insectivory may well be surprisingly great: such discoveries would be congruent with repeated assertions that insect ivory in larger primates is generally highly underestimated (McGrew, 2001).

We have demonstrated that uacaris positively select infested fruits of at least some species of diet plant, and that the larvae may represent a significant proportion of the mass of the ingested object. While our results do not indicate that positive selection of infested fruits occurs in every instance, it shows that such selection does occur, and does so in species that are important in the overall diet. The study also shows that selection is not based on simple presence/absence of insect larvae. The situation is complex, and can only be understood with further detailed work that should include the relative protein content and nutrient profiles of the insect larvae involved and the chemical changes (if any) occurring in fruits they infest. It would also be interesting to know how uacaris detect which fruits are infested. Bravo (2012) found that Black howlers spent longer feeding on infested trees and actively selected between moth and weevil-ingested trees. Whether uacaris use similar mechanisms could also be tested. The selection of a sub-section of apparently similar fruits seeds may mean simple optimal foraging theory predictions are not obeyed in relation to size of patch/ canopy or density of fruits. This is especially pertinent since more fruits may mean higher levels of infestation (Courtney & Manzur, 1985). The current method of estimating selectivity could also be improved in future studies by comparing the percentages of infested fruits on canopies to which uacaris have access and those from which they are excluded by large canopy-covering nets.

ACKNOWLEDGEMENTS

Field work undertaken with CNPq-IBAMA Protected Area Study License 138/2006. IBAMA-Manaus issued monthly park research permits. Funding generously provided by: American Society of Primatologists, Columbus Zoo Conservation Fund, Sophie Danforth Conservation Fund, LSB Leakey Foundation (US), Leakey Fund (UK), Laurie Shapley, Margot Marsh Foundation, Oregon Zoo Conservation Fund, Percy Sladen Memorial Fund, Pittsburgh Zoo and Aquarium Conservation Fund, Primate Action Fund, Primate Conservation Inc., Roehampton University, Wildlife Conservation Society. Technical assistance was provided by Fundação Vítoria Amazônica. Wealsothank Eliana dos Santos Andrade (logistics), Eduardo do Souza, Maria de Bom Jesus, Roberto Morreira (guides), IBAMA staff at Jaú, and Drizelinamara-Maria Yamomoto-Schwartz. Dick Vane-Wright (University of Kent Canterbury) identified the Lepidoptera. This is contribution number 16 from the Igapó Study Project and contribution number 9 from the Amazon Mammal Research Group.

REFERENCES

[1] Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **49**, 227-267.

[2] Ayres, J.M.(1986). Uakaris and Amazonian Flooded Forest. Unpublished PhD Thesis, University of Cambridge.

[3] Ayres, J.M. (1989). Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes. J. Human Evol.* **18**, 697-716.

[4] Ayres, J.M. & Nessimian, J.L**.** (1982). Evidence for insectivory in *Chiropotes satanas. Primates* **23**, 458-459.

[5] Barnett, A.A. (2005). *Cacajao melanocephalus. Mammalian Species* #**776**, 1-6.

[6] Barnett, A.A. (2010). Diet, habitat use and conservation ecology of the golden-backed uacari, *Cacajao melanocephalus ouakary*, in Jaú National Park, Amazonian Brazil. Unpublished PhD Thesis, Roehampton University.

[7] Barnett, A.A., de Castilho, C.V., Shapley, R.L. & Anicácio, A. (2005). Diet, habitat selection and natural history of *Cacajao melanocephalus ouakary* in Jaú National Park, Brazil. *Int. J. Primatol.*, **26**, 949-969.

[8] Barnett, A.A., Ronchi-Teles, B., Almeida, T., Silva Sousa, W., Deveny, A., Schiel-Baracuhy, V., Spironello, W.R., Ross, C., MacLarnon, A. (2013). Arthropod predation by the golden-backed uacari, *Cacajao melanocephalus ouakary* (Pitheciidae), in Jaú National Park, Brazilian Amazonia. *Int. J. Primatol.* **34**, 470-485.

[9] Barnett, A.A., Bowler, M., Bezerra, B.M. & Defler, T. (2013). Ecology and behavior of uacaris (genus *Cacajao*). In: Veiga LM, Barnett AA, Ferrari S, Norconk M, eds. *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris.* Cambridge: Cambridge University Press, 151-172.

[10] Barnett, A.A., Santos, P., Boyle, S. & Bezerra, B.M. (2015). An improved technique for in-field quantification of the force required by primates for the dental penetration of fruit. *Folia Primatol.* **86**, 398-410.

[11] Barnett A.A., Bezerra B.M., Spironello W.R., Shaw P., Ross C., & MacLarnon A. (2016). For aging with finesse: a hard-fruit-eating primate selects weak estare as as bite sites. *Am. J. Phys. Anthropol.* 160 :113-125.

[12] Bezerra, B.M., Barnett, A.A., Souto, A. & Jones, G. (2011). Ethogram and natural history of golden - backed uakaris (*Cacajao melanocephalus*). *Int. J.Primatol.* **32**, 46-68.

[13] Borowicz, V. A. (1988). Do vertebrates reject decaying fruit? An experimental test with *Cornus amomum* fruits. *Oikos* **53**, 74-78.

[14] Bravo, S.P. (2012). From which *Ocotea diospyrifolia* trees does *Alouatta caraya* (Primates, Atelidae) eat fruits? *J. Trop. Ecol.* **28**, 417- 420.

[15] Bravo, S.P. & Zunino, G.E. (1998). Effects of black howler monkey (*Alouatta caraya*) seed ingestion on insect larvae. *Am. J. Primatol.* **45**, 411–415.

[16] Bryer, M.A.H., Chapman C.A., Raubenheimer, D., Lambert, J.E. & Rothman, J.M. (2015). Macronutrient and energy contributions of insects to the diet of a frugivorous monkey (*Cercopithecus ascanius*), *Int. J. Primatol*. **36**, 839–854.

[17] Buchholz, R. & Levey, D.J. (1990). The evolutionary triad of microbes, fruits, and seed dispersers: an experiment in fruit choice by cedar waxwings, *Bombycilla cedrorum*. *Oikos* **59**, 200-204.

[18] Burger, A.E. (1987). Fruiting and frugivory of *Cornus canadensis* in boreal forest in New found land. *Oikos* **49**, 3-10.

[19] Cipollini, M.L. & Stiles, E.W. (1993). Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. *Ecology 74*, 751–762.

[20] Chivers, D.J. (1969). On the daily behaviour and spacing of howling monkey groups. *Folia Primatol.* **10**, 48-102.

[21] Courtney, S. P., & Manzur, M. I. (1985). Fruiting and fitness in *Crataegus monogyna*: the effects of frugivores and seed predators. *Oikos* **44**, 398-406.

[22] Desouhant, E. (1998). Selection of fruits for oviposition by the chestnut weevil, *Curculio elephas. Entomol. Experim. Applic.* **86**, 71-78.

[23] Drew, R.A.I. (1988). Amino acid increases in fruit infested by fruit flies of the family Tephritidae. *Zool. J. Linn. Soc.* **93**, 107-112.

[24] Dreyer, W. (1984). Zur Biologic wichtiger Weiss dorninsektenundihrer Parasiten. *Z. Entomol.* **97**, 71-78.

[25] Ferrari, S.F. (1988). The behaviour and ecology of the buffy-headed marmoset, *Callithrix flaviceps* (O. Thomas, 1903). PhD Thesis, University College, London.

[26] Ferrari, S.F., Guedes. P.G., Figueiredo. W. & Barnett, A.A. (2014). Reconsidering the nomenclature of the black-faced uacaris (*Cacajao melanocephalus* group, *sensu* Hershkovitz, 1987) from the northern Amazon basin. *Zootaxa 3866*, 357-370.

[27] Forget, P.M., Munoz, E. & Leigh Jr, E.G. (1994). Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* **26**, 420-426.

[28] Gentry, A.H. (1993).*A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru) with Supplementary Notes.* Chicago: University of Chicago Press.

[29] Hern, A. & Dorn, S. (2001). Induced emissions of apple fruit volatiles by the codling moth: changing patterns with different time periods after infestation and different larval instars. *Phytochemistry* **57**, 409-416.

[30] Herrera, CM. (1984). Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of *Berberis hispanica*. *Oikos* **42**, 166-170.

[31] Herrera, CM. (1989). Vertebrate frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest. *Oikos* **54**, 185-188.

[32] Janzen, DH. (1977). Why fruits rot, seeds mold and meat spoils. *Am. Nat.* **111**, 691-711.

[33] Julliot, C. (1996). Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *Int. J. Primatol.* **17**, 239-258.

[34] Junk, WJ. (1997). *The Central Amazon Floodplain: ecology of a pulsing system.* Springer, Ecological Studies series.

[35] Kamel, AH. (1982). Faba bean pests in Egypt. In: Hawtin G., Webb C, eds. *Faba Bean Improvement: Proceedings of the Faba Bean Conference held in Cairo, Egypt, March 7-11, 1981.* Springer Netherlands, Dordrecht (World Crops: production, utilization & description series), 271-275.

[36] Kinzey, W.G. & Norconk, M.A. (1993).Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int. J. Primatol.* **14**, 207-227.

[37] Link A. (2003). Insect-eating by spider monkeys. *Neotrop. Prim.* **11**, 104-107.

[38] McGrew WC. (2001). The other faunivory: primate insectivory and early human diet. In: Stanford CB, Bunn HT, eds. *Meat-eating and Human Evolution*, Oxford: Oxford University Press, 160-178.

[39] Mittermeier RA, Konstant WR, Ginsberg H, van Roosmalen MGM, Cordeiro da Silva E Jr. (1983). Further evidence of insect consumption in the bearded saki monkey, *Chiropotes satanas chiropotes. Primates* **24**, 602-605.

[40] Norconk MA, Wright BW, Conklin-Brittain NL, Vinyard CJ. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation* (Garber P, Estrada A, Bicca-Marques JC, Heyman EW, Strier KB (eds.) Springer: New York. pp. 279-319

[41] Norconk MA., Setz E.Z. (2013). Ecology and behaviour of saki monkeys (genus *Pithecia*), In: Veiga LM, Barnett AA, Ferrari S, Norconk M, eds. *Evolutionary Biology and Conservation of Titis, Sakis and Uacaris*. Cambridge: Cambridge University Press, 262-271.

[42] Peguero G, Espelta J.M. (2013). Evidence for insect seed predator dynamics mediated by vertebrate frugivores. *Rev. Chilena Hist. Nat.* **86**, 161-167.

[43] Piper, J.K. (1986). Seasonality of fruit characters and seed removal by birds. *Oikos***46**, 303-310.

[44] Prasifka, J.R., Hulke, B.S. & Seiler, G.J. (2014). Pericarp strength of sunflower and its value for plant defense against the sunflower moth, *Homoeosoma electellum. Arthropod-Plant Interact.* **8**, 101-107

[45] Redford, K.H., Bouchardet da Fonseca, G.A. & Lacher, T.E. Jr. 1984.The relationship between frugivory and insectivory in primates. *Primates* **25**, 433-440.

[46] Ribeiro, S.J.E.L.and 13others. (1999). *Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra firme na Amazonia Central.* Manaus: DFID-Instituto Nacional de Pesquisas da Amazônia.

[47] Rocha VJ, dos Reis NR & Sekiama ML. 1998. Uso de ferramentaspor *Cebusapella* (Linnaeus) (Primates, Cebidae) paraobtenção de larvas de coleopteran queparasitam sementes de *Syagrus romanzoffianum* (Cham.) Glassm. (Arecaceae). *Revista Brasileira de Zoologia* **15**, 945-950.

[48] Rodríguez, A., Alquézar, B. & Pena, L. (2013). Fruit aromas in mature fleshy fruits as signals of readiness for predation and seed dispersal. *New Phytol.* **197**, 36-48.

[49] Roth, L.M. &Eisner, T. (1962). Chemical defenses of arthropods. *Ann. Rev. Entomol.* **7**, 107-136.

[50] Sallabanks, R. & Courtney, S.P. (1992). Frugivory, seed predation, and insect-vertebrate interactions. *Ann. Rev. Entomol.* **37**, 377-400.

[51] Sazima, I. (1989). Peach-fronted Parakeet feeding on winged termites. *Wilson Bull.* **101**, 656-651.

[52] Schaller, A. (2008). *Induced Plant Resistance to Herbivory*. Springer, Dordrecht.

[53] Schiel, N., Souto, A., Huber, L. & Bezerra, B. (2010). Hunting strategies in wild common marmosets are prey and age dependent. *Am. J. Primatol.***72**, 1039-1046.

[54] Scott, J.K. & Black, R. (1981).Selective predation by White-tailed Black Cockatoos on fruit of *Banksia attenuata* containing the seed-eating weevil *Alphitopis nivea. Wildlife Res.* **8**, 421-430.

[55] Semel, B. & Anderson, D.C**.** (1988). Vulnerability of acorn weevil (Coleoptera: Cuculionidae) and attractiveness of weevil infested *Quercusalba* acorns to *Peromyscus leucopus* and *Blarnia brevicauna. Am. Midl. Nat.* **119**, 385-393.

[56] Siegel, S. (1956).*Non-parametric Statistics for the Behavioural Sciences*. McGraw-Hill. New York.

[57] Silvius, K.M. (2002). Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or grubivory? *J. Trop. Ecol.* **18**, 707-723.

[58] Southgate, B. (1979). Biology of the Bruchidae. *Ann. Rev. Entomol.* **24**, 449-473.

[59] Steele, M.A., Hadj-Chikh, L.Z. & Hazeltine, J. (1996). Caching and feeding by *Sciurus carolinensis*: responses to weevil-infested acorns. *J. Mamm.* **77**, 305-314.

[60] Sterling, E.J.(1994). Aye-ayes: specialists on structurally defended resources. *Folia Primatol.* **62**,142-154.

[61] Tashiro, Y. (2006). Frequent insectivory by two guenons (*Cercopithecus lhoesti* and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *Primates* **47**, 170-173.

[62] Toju, H., Ueno, S., Taniguchi, F. & Sota, T. (2011). Meta population structure of a seed–predator weevil and its host plant in arms race co evolution. *Evolution* **65:** 1707-1722.

[63] Tutin, C.E., Parnell, R.J. & White, F. (1996). Protecting seeds from primates: examples from *Diospyros* spp. in the Lopé Reserve, Gabon. *J. Trop. Ecol.* **12**, 371-384.

[64] Utzurrum, R.C.B. & Heideiman, P.D. (1991). Differential ingestion of viable vs. nonviable *Ficus* seeds by fruits bats. *Biotropica* **23**, 311–312.

[65] Valburg, L.K. (1992*a*). Eating infested fruits: interactions in a plant-disperser-pest triad. *Oikos* **65**, 25-28.

[66] Valburg, L.K. (1992*b*). Feeding preferences of common bush-tanagers for insect-infested fruits: avoidance or attraction? *Oikos* **65**, 29-33.

[67] Veiga, L.M. & Ferrari, S.F. (2006). Predation of arthropods by southern bearded sakis (*Chiropotes satanas*) in eastern Brazilian Amazonia. *Am. J. Primatol.* **68**, 209-215.

[68] Waldhoff, D., Saint-Paul, U. & Furch, B. (1996). Value of fruits and seeds from the floodplain

forests of Central Amazonia as food resource for fish. *Ecotropica* **2**, 143-156.

[69] Weiblen, G.D. (2002). How to be a fig wasp. *Ann. Rev. Entomol.* **47**, 299-330.

Appendix1A. *Field studies where insects in fruit recorded in diet of larger (> 2kg) Neotropical primates.*

Neotropical primate species	% of insects in diet*or* notes	Reference
Alouatta caraya	Up to 74% of fruit of one Lauraceous tree species infested, either with weevil or lepidopteran larvae	Bravo, S.P. (2012). From which *Ocotea diospyrifolia* trees does *Alouatta caraya* (Primates, Atelidae) eat fruits? *J. Trop. Ecol.* **28**, 417-420.
Cacajao calvus calvus	Up to 70% of seeds from plant species infested with beetle larvae	Ayres, J.M. (1989). Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *J. Human Evol.* **18**, 697-716.
Lagothrix lagothricha. *lagothricha*	No insects found in stomach of *C. torquatus*. But, at least 133 individual insects found in a *L. l. lagothricha* stomach, including cicadas ‘’unlikely to have been inadvertently consumed while the animal was eating fruit’’.-	Milton, K. & Nessimian, J.L. (1984). Evidence for insectivory in two primate species (*Callicebus torquatus lugens* and *Lagothrix lagothricha lagothricha*) from northwestern Amazonia. *Am. J. Primatol.* **6**, 361-371.
Sapajus apella	Capuchins positively selecting infested fruits even to the extent of using tools to extract the concealed larvae.	Rocha, V.J., dos Reis, N.R. & Sekiama, M.L. (1998). Uso de ferramentas por *Cebus apella* (Linnaeus) (Primates, Cebidae) para obtenção de larvas de coleoptera que parasitam sementes de *Syagrus romanzoffianum* (Cham.) Glassm. (Arecaceae). *Rev. Bras. Zool.* **15**, 945-950.

Appendix1B: *Captive studies where insects in fruit found to be chosen disproportionately by primates, so indicating positive selection of fruits containing insects.*

Neotropical primate species	% of insects in diet *or* notes	Reference
Callithrix penicillata	Captive individuals preferentially selected bananas into which *Tenebrio* beetle larvae inserted	Redford, K.H., Bouchardet da Fonseca, G.A. & Lacher, T.E. Jr. (1984). The relationship between frugivory and insectivory in primates. *Primates* **25**, 433-440.

Appendix2. *Behaviour recording protocols*

Sampling Methodology

We used binoculars to obtain behavioral data with sequential instantaneous scan sampling (Altmann, 1974). Behavioral data collection was commenced only after a five-month habituation period, over which the range at which human observers were tolerated declined from 30m to 10m. Because of the speed at which uacaris move in the canopy (Barnett, 2010), as well as inter-individual distances that often exceeded 10 body-lengths, it was difficult to record data reliably from more than three animals simultaneously. Consequently, if uacari group size exceeded three, we chose the nearest three animals and conducted scans every 30 seconds for five sequential minutes following contact, with each of the three chosen animals being sequentially point-sampled during this time. Such a sampling regimen gave a maximum of 33 records (i.e. 11 per animal) during each five-minute period. If, during the sampling time period, any target animal was not visible at the moment of recording, we marked that record as ‘out of sight’. If no animals were visible for three sequential scans (i.e. 3 x 30-seconds) then we terminated the observational block. One-minute intervals separated observational blocks, then, after a five-second pause to guard against picking the most visible behaviour, we began observations again.

Feeding Records

Following Tutin *et al.* (1996), we supplemented visual identifications of diet items made at the time of ingestions with collection directly beneath feeding trees of diet item remnants (orts) found immediately following feeding by uacaris. We defined a feeding record as any behaviour which resulted in a uacari placing a potentially digestible item in its mouth. To avoid repeat counting of eaten items, we removed such fallen floating material once it had been enumerated. To avoid the possibility of counting the same feeding event twice (i.e. first as a viewed feeding event and then again as an ort), we calculated the total of behavioral feeding records for an invertebrate taxon as the number of chewed, dropped food items retrieved floating below a tree, minus the number of behavioural observations of that taxon being eaten by *C. ouakary* in the same tree.

Appendix3. *Details of Fruit Acquisition and infestation estimation*

Collecting Fruit

We collected fruits that had been eaten by uacaris from directly under feeding trees immediately after the feeding primates had jettisoned them (so avoiding loss to frugivorous fish). We also collected complete and un eaten fruits to determine infestationand for penetrability analysis. Uacaris mainly eat unripe seeds, we therefore collected complete unripe fruits directly from the canopy of uacari feeding trees, either with a pruning hook or by climbing and plucking. To ensure comparability of ripeness stage, we used those that had the same size, weight, color, scent, and husk penetrability as those eaten by uacaris when selecting fruits for analysis. Subsequently, these fruits were destructively sampled for their infesting insects. Fruit were considered infested if arthropod larvae were detected in either these or surrounding pulp. Only fruits of species known to being tested and so directly involved in the diet were included in the study.

Estimating Infestation

To test if uacaris were actively selecting infested or non-infested seeds; we compared the percentage of infested fruits on trees with that in fresh feeing debris. We considered that when on-tree infestation rates exceeded those of the debris, this indicated active selection of infested seeds by uacaris, when the two ratios were qualt here was no selection, and when on-tree infestation rates were less than those in the feeding debris, that this indicated active selection of non-infested seeds.

To test if uacaris were eating infested fruits year-round, care was taken to collect diet fruits in all three phases. Fruits were always collected and examined at the maturational stage at which *C. ouakary* ate them.

Appendix4. *Number of fruit feeding records by* Cacajao ouakary *on the 26 plant species involved in this study that had fruits infested by larval insects (from the total 101 species and 11,902 feeding records reported by Barnett, 2010).*

Species	Total Number of Feeding Records[1] (infested and non-infested records combined)	Rank in Diet (fruit only)
Amanoa oblongifolia	200	13
Bombacopsis macrocalyx	32	54
Calophyllum brasiliense	8	92
Calyptranthes c.f. *creba*	160	18
Chaunochiton loranthoides	277	9
Diospyros cavalcanteii	51	40
Duguettia sp.	5	98
Duroia aquatica	17	73
Duroia velutina	220	11
Elaeoluma glabrescens	152	20
Eschweilera tenuifolia	1676	2
Eugenia sp.	53	38
Inga obidensis	49	42
Inga rhynchocalyx	10	86
Licania heteromorpha	41	47
Mabea nitida	397	6
Macrolobium acaciifolium	168	17
Mouriri guianensis	43	50
Myrcia sp.	27	59
Panopsis rubescens	50	41
Parkia discolor	15	77
Protium sp.	4	98
Pouteria elegans	565	4
Pouteria sp.	190	14
Sloanea sp.	16	75

[1] *a ´feeding record´ is defined as a record of the ingestion of a single fruit or fruit part (e.g. seed, aril), independent of the relative size or weight of the components in comparison to others on the list.*

Appendix5. *Examples of gall-eating in primates*

Taxon	Reference
Lemurs	
Daubentonia madagascariensis	Pollock, J.I., Constable, I.D., Mittermeier, R.A., Ratsirarson, J. & Simons, H. (1985). A noteonthe diet and feeding behavior of the aye-aye, *Daubentonia madagascariensis. Int. J. Primatol*. **6**, 435-447.
Indri indri	Britt, A., Randriamandratonirina, N.J., Glasscock, K.D. & Iambana, B.R. (2003). Diet and feeding behaviour of *Indriindri* in a low-altitude rainforest. *Folia Primatol.* **73**, 225-239.
Old World Monkeys	
Erythrocebus patas pyrrhonotus	Isbell, L.A. (1998). Diet for a small primate: Insectivory and gummivory in the (large) patas monkey (*Erythrocebus patas pyrrhonotus*). *Am. J. Primatol.* **45**, 381-398.
Macaca fuscata	Hanya, G. (2004). Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *Int. J. Primatol*. **25**, 55-71.
Macaca radiata	Krishnamani, R. (1994). Diet composition of the bonnet macaque (*Macaca radiata*) in a tropical dry evergreen forest of southern India. *Trop. Biodiv.* **2**, 285-302.
Papio anubis	Rose, M.D. (1977). Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* **18**, 59-116.
Presbytis entellus	Srivastava A. (1991). Insectivory and its significance in langur diets. *Primates* **32**, 237-241; Sugiyama,Y. (1964). Group composition, population density and some socio logical observations of hanuman langurs. *Primates* **5**, 7-37.
Apes	
Gorilla gorilla beringei	Vedder, A.L. (1984). Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. *Am. J. Primatol*. **7**, 73-88; Watts, D.P. (1984). Composition and variability of mountain gorilla diets in the central Virungas. *Am. J. Primatol*. **7**, 323-356
Pan t. troglodytes	Tutin, C.E. & Fernandez, M. (1993). Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. *Am. J. Primatol*. **30**, 195-211.
New World Primates	
Ateles chamek	Wallace, R.B. (2005). Seasonal variations in diet and foraging behavior of *Ateles chamek* in a southern Amazonian tropical forest. *Int. J. Primatol*. **26**, 1053-1075.
Callicebus oenanthe	De Luyckyer, A.M. (2012). Insect prey for aging strategies in *Callicebus oenanthe* in northern Peru. *Am. J. Primatol*. **74**, 450-461.
Callicebus torquatus	Milton, K. & Nessimian, J.L. (1984). Evidence for insectivory in two primate species(*Callicebus torquatus lugens* and *Lagothrix lagothricha lagothricha*) from north western Amazonia. *Am. J. Primatol*. **6**, 361-371.
Chiropotes satanas	Frazão, E. (1991). Insectivory in free-ranging bearded saki (*Chiropotes satanas chiropotes*). *Primates* **32**, 243-245. Veiga LM & Ferrari SF. (2006). Predation of arthropods by southern bearded sakis (*Chiropotes satanas*) in eastern Brazilian Amazonia. *Am. J. Primatol*. **68**, 209-215.
Lagothrix lagotricha	Milton K, Nessimian JL. 1984. (ibid).