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**The bitter end: primate avoidance of caterpillar-infested trees in a central Amazon
flooded forest.**

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ABSTRACT:

Animal-plant interactions are often mediated by chemical compounds. It has been widely reported that herbivore damage to plants induces chemical defenses which may then affect subsequent interactions with both invertebrate and vertebrate herbivores. Our study investigated the effects of the interaction between larvae of an unidentified Nymphalid butterfly and the tanimbuca tree (*Buchenavia ochroprumna* Eichler Combretaceae) on subsequent folivory by a primate, the golden-backed uacari (*Cacajao ouakary* Spix, 1823, Pitheciidae). Primate feeding observations, records of the extent of Nymphalid/*Buchenavia* interactions and tree distribution occurred in Jaú National Park, Amazonas State, Brazil. Ivlev Electivity Index values showed that uacaris strongly rejected trees infested by caterpillars (- 0.68), while uninfested trees were highly selected by them (+ 0.84). Given this behavior, we suggest that uacari monkeys may be deterred by (i) caterpillars; (ii) change in leaf chemical composition induced by caterpillars; (iii) or a combination of both.

KEY WORDS: avoidance – *Buchenavia ochroprumna* – *Cacajao ouakary* – igapó – induction - Lepidopteran herbivory - secondary compounds

INTRODUCTION

Primates food item choices are based on a variety of factors including abundance of preferred and fallback foods according to seasonal availability (Hanya and Bernard 2012; Matsuda et al. 2017), chemical properties (DeGabriel et al. 2014), nutrient profiles (Ganzhorn et al. 2016), and optimal foraging constraints (Matsuda et

al. 2013). Of these, protein concentrations may be especially important when soil nitrogen is low, and hence plant protein availability in the habitat is limited (Ganzhorn et al. 2016).

Herbivorous animals can have both direct and indirect interactions with plant chemical compounds, and these may be derived from either primary or secondary metabolism. Primary metabolic compounds are involved in vital activities such as growth and development, whilst the products of secondary metabolism operate mainly as mediators of plant interactions (Croteau et al. 2000; Harborne 2001; Iason 2005; Iason and Villalba 2006; Mithöfer and Boland 2012) (Supplemental Table S1).

In primates, most reported interactions with plants are direct, with tannins/protein ratios influencing leaf choice by folivorous primates at the between-species level, though there have also been studies of leaf-choice between conspecific trees, and at the within-individual level (Supplemental Table S2). Indirect interactions exist, but are much more rarely reported (Supplemental Table S2).

While there are many examples of induced chemical defences subsequently deterring both invertebrates and vertebrates (Supplemental Table S3), such a system has, to our knowledge, never been reported between a primate species and its food plant. Here we report such a possible interaction, involving the tanimbuca tree (*Buchenavia ochroprumna* Eichler, Combretaceae), the larvae of a currently unidentified Nymphalid butterfly, and the golden-backed uacari monkey (*Cacajao ouakary* Spix, 1823, Pitheciidae) in seasonally-flooded forests in central Brazilian Amazonia.

Other studies at Jaú have found that (i) for some plant species, uacaris select seeds with insects inside them (Barnett 2010; Barnett et al. 2017), and that (ii) in the season of low

fruit availability they eat insects, in addition to large volumes of leaves (Barnett 2010), and that (iii) these include several types of lepidopteran larvae (Barnett 2010; Barnett et al. 2013). Consequently, based on the hypothesis that uacaris are using leaves and insects as fall-back foods in the season of low fruit availability, we tested the following predictions: (1) Uacaris will visit *B. ochroprumna* trees with both new leaves and caterpillars, and will prefer such trees to those with no new leaves or trees with new leaves but without caterpillars; (2) At infested trees both the leaves and the caterpillars will be eaten more frequently than one single item alone; and (3) The closest tree to a feeding tree will be the next feeding tree, but only if it bears caterpillars.

METHODS

Study site

Field observations were made between Oct 2006 and April 2008 in Jaú National Park, (1°53'15.96"S 61°41'25.46"W), a 2.3 million ha protected area between the Unini and Carabinani rivers in Brazilian Amazonia, situated some 220 km west of the city of Manaus on the south bank of the Rio Negro, Amazonas State, Brazil (Fig. 1). Habitats include rainforest (80%+), igapó (12%), white sand vegetation types (2%), palm and aroid swamps (2%), and disturbed land (<1%: FVA-IBAMA 1998). The peak rainy season is between November and April, the minima between June and September. The river level is at its peak in April-September, and its nadir occurs between October-January (Ferreira 1999).

At Jaú, field observations were made in igapó forest. This is a seasonally flooded forest type present on the margins of blackwater rivers in the Amazon basin. It forms a narrow band of vegetation (rarely more than 200 m wide), and has a strong seasonal flood-pulse

that lasts for up to nine months of the year, during which waters may attain heights of 10 m above their lowest mark (Haugaasen and Peres 2006). Igapó forest trees vary in their tolerances to inundation duration (Parolin et al. 2005), which results in compositionally-distinct tree assemblages at different distances parallel to the river bank (Barnett et al. 2015).

Fig 1 here

Species

The plant

The tanimbuca tree (*B. ochroprumna*) occurs principally in western Amazonia (Rio Negro and western Orinoco river basins) (Marquete and Loiola 2015). It is a common tree of seasonally flooded forests on the margins of blackwater rivers in the Amazon basin (igapó, *sensu* Prance 1979).

Buchenavia ochroprumna has medium tolerance to flooding and, as such, is found in the middle zone of the igapó forest (Barnett 2010). It grows to some 15 m, has a characteristic inverse-cone shape when fully emergent from floodwaters (the result of flood-time grazing by herbivorous fish) and spatulate (sometimes bluntly cunate) coriaceous leaves that occur in clusters of terminal whorls of five to nine leaves (A.A. Negreiros, A.A. Barnett, unpublished data) (Fig. 2a and b). All individuals of *B. ochroprumna* at Jaú synchronously shed their leaves in June, then flush new leaf growth within two weeks (A.A. Barnett, unpublished data). Leaves take 30-40 days to reach full hardness and size (some 4.5 cm), during which time they are preyed upon intensively by the larvae of a Nymphalid lepidopteran (Barnett 2010).

Fig 2 here*The insect*

The Nymphalid caterpillars were dark mottled brown and smooth skinned, but with irregular stiff protruding spikes (Fig. 3). Mean mass and length of 32 animals in the final instar, were 295.15 mg, (SD $\pm$ 76.64, range 186-416) and 22.67 mm (SD $\pm$ 2.0, range 19.2-25.4), respectively. A count of the number of caterpillars on 73 infested leaf whorls of *B. ochroprumna* found a mean of 3.08 caterpillars per whorl (SD $\pm$ 1.73, range 1-7).

Fig 3 here*The primate*

The golden-backed uacari (*C. ouakary*) is a medium-sized primate (mean mass 3.5 kg; mean body length (mm) 389 (f), 414 (m): Hershkovitz 1987) whose principal habitat is the blackwater seasonally-flooded river-margin forests (igapó, *sensu* Prance 1979) of the Rio Negro Basin, Amazonia, South America (Barnett 2005). The home range can exceed 2 km² (Bezerra, Souto and Jones 2010). The diet is principally immature seeds from hard, unripe fruits (Barnett et al. 2005, 2013, 2018). However, in those months of the year when, as a result of the highly-seasonal phenology of igapó, there is little fruit available, these primates become predominantly folivorous (Barnett 2010). At this time, the leaves and buds of tanimbuca constitute 10.9% (118/1084) of all *C. ouakary* foliage-based feeding records (Barnett 2010). Uacari group size varies with resource availability. However, groups are often widely dispersed and adult individuals generally forage singly in tree canopies (Barnett 2010), though coordinated in their overall movements by near-continuous contact calls (Bezerra et al. 2010).

Field methods

As part of a broader study of the foraging ecology (see Bezerra et al. 2010; Barnett and Shaw 2014; Barnett et al. 2012, 2013, 2016), golden-backed uacaris were followed through their flooded igapó habitat in a wooden canoe, and, following Altmann (1974), feeding observations were made using both scan sampling and *ad libitum* observations.

Within igapó, five 0.25 ha botanical inventory and phenology plots (hereafter called BIP plots) were set up, positioned to cover the range of inundation durations. In each, all woody plants above 10 cm DBH (Diameter at Breast Height) were tagged and identified. Phenology (leaf flush, flowering and fruiting) was recorded once-a-month from December 2006 to November 2008, with all incidences and extents of insectivory on leaves noted as a part of standardized field protocol, which included a classification of infestation intensity in 20% increments. Feeding was defined as an item being placed in the mouth and ingested. For plants species from which uacaris ate leaves, individual plants were always checked for any leaf-damage that indicated recent prior herbivory. Both in and outside the study plots, trees on which uacaris fed were marked with numbered tags.

Tanimbuca trees were found in three of the five BIP plots, and uacaris were seen feeding in all three. Outside the BIP plots uacaris were seen feeding on tanimbuca at two other locations within the inundation-duration zone inhabited by this tree species. These were included in the study. For purposes of quantification, each was bounded by a 10 m buffer beyond 10 fed-upon trees in each plot, so forming a maximum convex polygon in which the number of tanimbuca, and other tree species could be counted and patterns in caterpillar infestation and uacari feeding quantified. These plots were named as Tanimbuca 1 and 2.

Distances were measured to nearest conspecific and to nearest known food tree of any species for each tanimbuca tree in which feeding was recorded. Incidences of trees being revisited were also recorded. For *B. ochroprumna*, whether the fed-upon tree was being eaten by caterpillars was recorded, as was (for non-infested trees) the distance to the nearest infested tree. We also measured whether the infested tree was the closest living individual of *B. ochroprumna* to the tree on which leaf-feeding had been recorded, or whether closer trees were present. If there were closer trees, the distance between them and the tree at which the uacari had fed and the tree with caterpillars was measured. Distances were measured with a tape-measure or a laser rangefinder (Bushnell Yardage Pro).

Infested trees were recognised by the presence of caterpillars on them, by the reduced size of new leaves, characteristic patterns of leaf-margin reduction and by the abundant frass, both falling from the trees and collecting beneath them on the surface of the slow-moving igapó waters (0.2 m hr⁻¹; Barnett and Shaw 2014).

Statistical analyses

Both predictions 1 (uacaris will visit more frequently *B. ochroprumna* with both new leaves and caterpillars) and 2 (at infected trees, uacaris will eat leaves and caterpillars more frequently than single item alone) were tested by calculating an Ivlev electivity index (Ivlev 1961) for fed-upon trees (counting multiple visits as one). This index compares the relative frequency of used items in the diet with their relative frequency in the habitat. Ivlev's index ranges from -1 to +1, with species used by the animal at parity to their relative frequency in the habitat having an electivity index of 0. Items with a use frequency exceeding that in the habitat sample are considered to be positively selected (and so have positive value), while

those used at less than parity will have a negative value. The index is calculated with the equation $r^i - p^i / r^i + p^i$ where r^i is percentage of item i in the diet and p^i is its percent composition in the habitat.

We also compared the frequency of eaten infested trees with their frequency among the total sample of 94 tanimbuca trees present in the five 0.25 ha igapó phenology and botanical composition study plots. For that we summed the counts of each *B. ochroprumna* category (eaten uninfested, eaten infested, uneaten uninfested and uneaten infested) of the five plots, and compared if uacaris feed more frequently on infested trees than expected by chance using chi-squared test.

To analyse the effect of proximity on feeding behavior, Euclidian distances between *Buchenavia* trees in which uacaris fed and nearest infested and non-infested *Buchenavia* trees and Euclidean distances between not-infested and caterpillar-infested trees were measured in three plots. Given the unbalanced sampling design, the data sets were compared with bootstrap permutation tests (sampling with replacement) based on 999 replicates implemented for each sampling plot (package “coin”: Hothorn et al. 2008). In each run the two distances measures were randomized and a t -value (from t -test) computed. We then compare the t -value of the 999 permutations with the observed value to calculate the probability that the observed value was different from chance. All analyses were done in R (R Core Team 2016).

RESULTS

Buchanavia ochroprumna comprised 6.6% of the 1,416 trees present in the five 0.25 ha igapó botany inventory and phenology study plots (94 individuals, the 4th. most common

tree). During the study period 77 of these trees (81.9%) were infested with caterpillars. Infestation levels on individual trees varied from low ($\leq 20\%$ of leaf whorls with signs of feeding) to extremely high ($\geq 80\%$). *Cacajao ouakary* individuals were recorded eating *B. ochroprumna* leaves on 118 occasions, making this species the 3rd most commonly eaten for leaves in the uacari diet. Feeding was observed at a total of 43 separate trees from both inside and outside the BIP plots. Of these only 3 (6.9% of all eaten trees) were infested, and these very lightly (5-10%). Inside the BIP study plots, all 17 uninfested trees were eaten plus two that were lightly infested. These comprised 19 of all the trees eaten (44.2%). Outside the BIP plots, Tanimbuca 1 and 2 (hereafter T1 and T2) had an additional 73 and 82 individual *B. ochroprumna* trees respectively, from which 61 (83.5%: T1) and 54 (65.8%: T2) were infested. T1 also had two uninfested trees on which uacaris were not seen to feed; one feeding tree was lightly infested. T2 also had 28 uninfested trees on which uacaris were not seen to feed at 18 (64.3%). Summing the three samples gave a mean infestation rate of 76.6% ($SD \pm 8.5$). Uacari use rate of uninfested trees varied from 100% (botanical study plot) to 83.3% (T1) and 35.8% (T2). Comparing these summed proportions for all uneaten infested vs. eaten uninfested vs. trees gives a combined Ivlev value of - 0.68, a value indicating extreme rejection of infested plants; while the value for eaten uninfested vs uneaten infested trees is + 0.84, indicating strong selection of uninfested trees.

Though uacaris feeding on lightly infested plants were seen to select only leaves and do so from uninfested parts of the tree, Prediction 2 could not be tested due to the very small sample size available ($n = 3$) (though this, in itself, reinforces the notion of that uacaris select against infested plants).

Uacaris did not feed in trees adjacent to infested trees. The closest record achieved for all three study plots was 9.7 m from such trees. The closest record between (non-infested) feeding trees was 36.9 m while the closest distance between uneaten (infested) trees was 4.1 m.

Mean distances between infested tanimbuca trees were small for the three plots in comparison with mean distances between non-infested tanimbuca trees in two of them (Table 1), showing that non-infested trees are rare or widely dispersed, while infested trees are common and/or clumped.

Mean distances between (non-infested) tanimbuca trees fed upon by uacaris and caterpillar infested trees were smaller than mean distances between all (non-infested) tanimbuca trees on which uacaris fed (Table 2). This indicates that uacaris are travelling further to feed from uninfested trees, reinforcing the data from the Ivlev Electivity Index that they are avoiding infested trees.

Table 1 and 2 here

DISCUSSION

Contrary to expectations based on dual-item diet optimization, *C. ouakary* did not feed more commonly on *B. ochroprumna* trees that had both caterpillars and new leaves. Instead, they almost completely avoided such trees, paying just a few visits to lightly infested trees (6.9% of feeding trees) where they ate leaves from branches well-away from those on which the caterpillars were feeding. It could be argued that the monkeys are avoiding infested trees because there is less of their preferred food—new leaves—on these trees. However, our data show that trees with more than 10% of new leaf whorls displaying

caterpillar damage were avoided. Given that they forage alone in a tree (but in calling contact distance with group members: Barnett 2010), the monkeys are avoiding trees with up to 90% of new leaf whorls untouched—meaning that there is definitely sufficient new plant material available on these trees for the uacaris.

Indeed, the tanimbuca trees from which uacaris eat leaves are significantly smaller than those fed on by caterpillars. As small trees are the only ones uninfested by caterpillars, this confirms that tanimbuca tree selection by uacaris is based on caterpillar avoidance, rather than resource patch size (AA Barnett, AA Negreiros; in preparation). Given this behavior, three explanations seem possible: uacaris were either deterred by the caterpillars, by some change in leaf chemical composition induced by caterpillar herbivory, or a combination of both.

Certainly, uacaris do not dislike caterpillars *per se*. Barnett et al. (2013) reported incidences of this species actively seeking the larvae of tortricid moths in still-unfolded young *Swartzia* leaves, and this primate also preferentially eats seeds infested with lepidopteran larvae, including members of the owlet moth (Noctuidae) and clear-wing moth (Sesiidea) families (Barnett 2010). Additionally, members of the genus *Chiropotes*, closely-related to *Cacajao*, have been reported eating hairy and spiny caterpillars, despite the obvious discomfort caused by handling them (Veiga and Ferrari 2006). However, uacaris have been observed to actively avoid social caterpillars of the saturniid *Arsenura armada* Cramer 1779 and aposomatic Dalceridae caterpillars, both of which are known to be highly toxic (Barnett 2010). They also avoided Lasiocampidae and Lymantriidae caterpillars. Many of the former are both hairy and toxic, while for the latter, the defence is both long barbed setae which are both irritant and toxic (Deml and Dettner 1995).

In addition, while choice based on avoidance of toxic or noxious chemicals has not yet been undertaken in the genus *Cacajao*, there are indications that some species known to be toxic are avoided, including the seeds of *Dipteryx* cf. *oppositifolia* (Aubl.) Forsyth f., *Swartzia laevicarpa* Amshoff and *S. polyphylla* DC. (seeds of these two genera being known for their high concentrations of toxic coumarins: Venugopala et al. 2013 and Dembitsky and Tolstikov 2004 - respectively). In addition, there is the fact that, since golden-backed uacaris only eat leaves in any quality for three months of the year, they are very much part-time folivores. As such they might well lack some of the detoxifying enzymes and gut bacterial flora found in primates whom leaves form a greater part of the diet (e.g. Lambert 1998) (though they do have some anatomical specializations to the gut that suggested partial folivory before this was known from the diet: MacLarnon et al. 1986). This may explain the fact that, apart from tanimbuca, the other group which predominated in the leaf diet of *C. ouakary* at Jaú was young Fabaceae leaves (Barnett 2010). Such items are known for high levels of nitrogen, and low levels of toxins (McKey 1994). Thus, *C. ouakary* may be acutely susceptible to induced changes in phytotoxin levels, such as might be facilitated by massed caterpillar attacks on *B. ochroprumna*, and which are known to produce robust responses from other plant species (*Pinus* spp.: Hodar et al. 2002; *Populus tremuloides* Michx.: Hemming and Lindroth 1995; *Quercus suber* L.: Staudt and Lhoutellier 2007).

In addition, there is the fact that uacaris avoided all 21 neighboring tanimbuca trees within a 10 m radius of the 77 infested trees included in the study, even when they were not infested with caterpillars. This opens the possibility that such trees were also showing induced phytochemical responses, as a result of volatile compounds released by neighboring trees (see Baldwin et al. 2006 and Heil and Karban 2010 for topic reviews).

In-field attempts to raise caterpillars to the imago stage, and so facilitate species (or genus) identification, were forestalled by ants. Thus, it is currently not possible to distinguish between the three options cited above, even if uacari avoidance of proximate uninfested trees favors the phytochemical option. The situation can only be fully examined with future studies that (i) identify the species (or genus) of Nymphalidae involved, so allowing analysis of potential chemical defenses and toxicity, (ii) assay the larvae for the presence of toxic and/or noxious compounds, and (iii) chemically analyse leaves of *B. ochroprumna* from both infested and uninfested trees to test the possibility that chemical responses induced by the herbivory of the caterpillars had made the leaves unpalatable to these part-time folivores.

Further analysis of this system could be highly relevant to an enhanced understanding of multi-species interactions in igapó ecology. Indirect invertebrate/vertebrate folivore interactions mediated by damage-induced phytochemical responses of the herbivorized plant, may not be uncommon in this habitat as heavy infestations of young *Eschweilera tenuifolia* Miers (Lecythidaceae) leaves by Hesperiid caterpillars were ignored by uacaris at Jaú, even as the primates ate the emerging leaves of uninfested conspecifics.

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Table 1: Distribution of infested and not-infested tanimbuca trees in the study site.

Plot	Distances between infested tanimbuca trees (mean ($\pm$ SD) in m)	Distances between non-infested tanimbuca trees (mean ($\pm$ SD) in m)	<i>p</i> -value
BIP 1	10.96 ($\pm$ 4.07)	55.91($\pm$ 21.7)	0.001
BIP 2	28.03 ($\pm$ 20.91)	35.97 ($\pm$ 18.23)	0.001
BIP 3	3.46 ($\pm$ 1.03)	All trees infested in this plot	NA

* *p*-values give the probability, based from bootstrap *t*-value resampling, that the distances between non-infested tanibuca trees are larger than distances between infested tanimbuca trees.

Table 2: Effect of existing caterpillar infestation on tanimbuca tree chosen by uacaris as sites for leaf-feeding.

plot	Distance between (non-infested) tanimbuca trees at which uacaris fed and the nearest caterpillar infested tanimbuca tree (mean ($\pm$ SD) in m)	Distance between (non-infested) tanimbuca trees at which uacaris fed and the next (non-infested) tanimbuca on which the uacaris fed (mean ($\pm$ SD) in m)	<i>p</i> -value
BIP 1	18.26 ($\pm$ 4.93)	46.28 ($\pm$ 7.43)	0.001
BIP 2	19.3 ($\pm$ 11.34)	56.68 ($\pm$ 12.51)	0.001
BIP 3	4.625 ($\pm$ 0.86)	8.16 ($\pm$ 2.95)	0.001

* *p*-values give the probability, based from bootstrap *t*-value resampling, that the distances between closest non-infested tanibuca trees at which uacaris fed and are larger than distances between non-infested tanibuca trees, which uacaris fed and the nearest tanibuca infested tree.

FIG. 1. Study site, showing Carabinani Research Base, Jaú National Park and its location in the Brazilian Amazon.

FIG. 2: *Buchenavia ochroprumna* Eichler showing (left) adult tree with characteristic inverted cone-shaped growth form, and (right) whorls of bluntly cunate new leaves in an uninfested tree. Photo credit: Waldir Heinrichs Caldas

FIG. 3: Nymphallid caterpillar feeding on new leaves of *Buchenavia ochroprumna* Eichler (left) and (right) leaves of *Buchenavia ochroprumna* Eichler showing characteristic damage patterns from caterpillar feeding that allowed infestation assessment at a distance of several meters. Photo credit: Waldir Heinrichs Caldas

FIG. 1. Study site, showing Carabinani Research Base, Jaú National Park and its location in the Brazilian Amazon.