

Terrestrial Foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: Is Choice of Seed Patch Size and Position Related to Predation Risk?

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Key Words

Diet · *Eschweilera* · Igapó · Predation-sensitive foraging · Pitheciidae · Seedling

Abstract

We analyse the behaviour of *Cacajao melanocephalus ouakary* feeding at patches of germinating seedlings in dried-out flooded forest. Seedlings of *Eschweilera tenuifolia* (Lecythidaceae) were the most commonly eaten (88.9%). Some seed patches were revisited over several days, while others were consistently ignored. We tested 3 predictions relating uacari terrestrial foraging behaviour to: (1) arboreal escape route proximity, (2) seed patch size choice and (3) temporal patterns of repeat exploitation. Comparison of fed-at and ignored patches revealed significant preferences for larger patches, and for those close to arboreal refuges but distant from dense ground-based vegetation. Support for these predictions is interpreted as evidence for predation risk-sensitive foraging.

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Introduction

While terrestrial activity in predominantly arboreal species appears quite common in Paleotropical primates (e.g. *Cercopithecus mitis* [Smith et al., 2008]; *Procolobus kirkii* [Nowak and Lee, 2011]), it is rarer, though not unknown, in the larger frugivorous Neotropical taxa (*Ateles* [Campbell et al., 2005]; *Brachyteles* [Tabacow et al., 2009]). However, it appears to be very infrequent in pitheciines, the clade of Neo-

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tropical primates that includes *Chiropotes* and *Pithecia* as well as *Cacajao*. Designated by Groves [2001] as a subfamily (Pitheciinae) of the Pitheciidae, the diet of pitheciines is dominated by immature seeds, supplemented with fruit pulp, leaves and flowers [Norconk, 2011]. The great majority of their feeding occurs in the upper forest canopy and emergent trees [Norconk, 2011]. In this group, terrestriality is either very rarely observed (*Chiropotes satanas* [Veiga, 2006]) or not recorded at all (*Chiropotes utahickae* [Bobadilla, 1998]; *Chiropotes chiropotes* [Boyle, 2008]).

The 3 pitheciine genera are broadly separated by habitat [Norconk, 2011]. *Pithecia* and *Chiropotes* are generally inhabitants of terra firme forest. Uacaris (genus *Cacajao*), though exceptions are known (e.g. some populations of *C. c. ucayalii* and *C. c. melanocephalus* [Boubli, 1997; Heymann and Aquino, 2010], respectively), principally inhabit forests that are seasonally flooded (*C. c. calvus* [Ayres, 1986]; *Cacajao melanocephalus ouakary* [Barnett, 2010]). In these, opportunities for on-the-ground activity are restricted to those few months when floodwaters recede. When recorded [Ayres, 1986], such activities generally involved feeding on the swathes of water-dispersed fruit and fish-dispersed seeds that germinate on the newly exposed forest floor [Parolin, 2001]. In Amazonian flooded forest tree communities, hydrochory and ichthyochory are the dominant dispersal modes; hence, fruit availability occurs in tight pulses that are synchronized across the community [Parolin et al., 2010]. In consequence, there is almost no fruit available in flooded forest tree canopies when forests are unflooded [Barnett, 2010].

While migration to the fruit-bearing canopy of terra firme forest is an option [Haugaasen and Peres, 2005a], exploitation of a superabundant resource is possible in dry igapó if terrestrial foraging options are pursued. However, this is potentially risky as predators such as the tayra (*Eira barbara*) and jaguar (*Panthera onca*) enter igapó at this time [Bodmer et al., 1998], probably attracted by the seasonal influx of such seed-predating rodents as the paca (*Cuniculus paca*) and agouti (*Dasyprocta* spp.). Thus, terrestrial foraging for uacaris can be potentially highly rewarding, but is also likely to be risky.

While confirmed predation events are generally rare, one likely reason for this is that primates consistently implement strategies to avoid it [Miller, 2002; Hart, 2007]. As has long been appreciated [De Vore and Hall, 1965; Terborgh, 1983; van Schaik et al., 1983], avoiding predation touches nearly all aspects of primate life from foraging, vigilance, cover use and time spent grooming [Hart, 2007], to choice of sleeping trees [Barnett et al., 2012]. Indeed, it may well be one of the major activities structuring the rhythm and form of the primate day [Ferrari, 2009]. Accordingly, much of a primate's foraging activity will be risk sensitive and involve balancing the quality of the available food resource against the possibilities of predation, and likelihood of escaping it [Miller, 2002; Ferrari, 2009]. As *C. m. ouakary* is essentially an arboreal primate, we would predict therefore that, when foraging terrestrially, golden-backed uacaris will: (i) choose patches with an *easy escape route* (prediction 1: uacaris will forage close to arboreal escape routes and distant from sites of potential predator concealment); (ii) choose patches with the *greatest seed density*/total number of seeds (prediction 2: that terrestrially foraging uacaris would also be expected to selectively choose food-dense patches rather than foraging generally on the forest floor; this will involve choosing areas of densely aggregated seedlings over areas where seedlings are sparse, and, when two seed patches are present in an area, uacaris will choose the larger), and (iii) make *repeat visits* to areas that have previously been safe (prediction 3: once a patch has

been discovered that meets criteria for safe foraging, it will be exploited repeatedly until the number of seeds is greatly diminished).

We tested these predictions with individuals of *C. m. ouakary* that were accessing seeds germinating on the floor of seasonally flooded forest (igapó) during the 4 months of the year when the igapó was not fully inundated. During this period the igapó habitat has few alternative food resources for uacaris [Parolin et al., 2010].

Taxonomic Note

In this paper, the scientific name for *Cacajao* sp. follows Hershkovitz [1987], since the precise appellation for some members of the genus is currently disputed [Boubli et al., 2008; Ferrari et al., 2009].

Methods

Study Site

The study was undertaken in terra firme (non-flooded) and igapó (seasonally flooded) forests [sensu Prance, 1979] at Jaú National Park, a 2,700,000 ha protected area in central Amazonian Brazil. The study was carried out between October 2006 and April 2008 and focused on the area between the first set of major rapids on the Jaú river (01°53'2" S, 61°40'4" W) and the village of Pataú (01°53'16" S, 61°44'3" W). Water levels in igapó have strong annual variation: flood waters peak in May-July (up to 15 m depth), and the forest floor is generally entirely dry only between December and January, and patchily boggy in November and February [Ferreira, 1997]. Data reported here were collected between November and February in 2006, 2007 and 2008. No terrestrial activity was ever observed in terra firme. General study results are reported in Barnett [2010].

Data Collection

Data on terrestrial feeding were collected as part of a broader study of *C. m. ouakary* habitat and diet selection [Barnett et al., 2008, 2011, 2012; Barnett, 2010], for which scan sampling was used to quantify diet choice and time budget, and ad libitum sampling was used to collect data on rare or previously unrecorded behaviours. Because terrestrial foraging (a) was not previously recorded for *C. m. ouakary* and (b) occurred in individual bouts that were always of short duration, all sampling relating to uacari behaviours on the ground were ad libitum. When terrestrial feeding was observed, food debris was searched for immediately after uacaris had ceased feeding. Uacaris were only observed feeding terrestrially at seedling patches (here defined as 'an area made visually distinct, and dimensionally circumscribed, by the enhanced density of seedlings within it') and were not seen to forage across the general forest floor. Accordingly, data were gathered on patch size and seedling density in exploited patches, and their proximity to overhanging boughs and large fallen trunks noted. Feeding sites (n = 7) were investigated directly following observation of feeding and the uacaris' subsequent departure.

Germinating seeds were identified by comparison with a photographic database compiled for general studies of *C. m. ouakary* diet [Barnett, 2010]. Seeds of many igapó tree species are water dispersed (hydrochorous) [Kubitzki and Zibursky, 1994], and tend to accumulate in drifts against floating logs and partly fallen trees. Both the obstacles and their impounded seed rafts slowly descend as the water level drops and the seeds finally contact the ground and germinate. This occurs in concentrated patches, and contrasts greatly with the rest of the forest floor, where undergrowth is almost non-existent and seedling density is low. This makes patches visually very distinct and easily defined. No comparable concentrations of germinating seeds were observed in terra firme.

It is common to use feeding traces to monitor foraging activity when multiple sites are being surveyed simultaneously [Sefczek et al., 2012]. Accordingly, we supplemented observations with data from seeds eaten in our absence. Such indirect sampling was facilitated by direct ob-

servation of uacaris feeding on germinating seeds, which allowed recognition of other patches where uacaris had been active so that their feeding activity could be easily distinguished from that of other seed-feeding terrestrial mammals (peccaries and rodents). Uacari bite marks lack the distinctive central ridge that characterizes the paired incisor-based gnawing of forest-floor rodents. Rodents normally bite a seed multiple times, uacaris only once. Peccaries ingest seeds whole, and their foraging pattern greatly churns the ground. This contrasts with uacari feeding, where the substrate remains intact and bitten seedlings and plumules are evident.

Though a common and conspicuous feature of the unflooded floor of igapó forest, not all seed patches showed evidence of uacari predation. The hypotheses that this reflected active choice by uacaris and that such choices were driven by predation were tested by comparing the characteristics of 7 seed patches at which feeding had occurred with other patches where it had not. To achieve this, for 2 days immediately following feeding observations we searched for seed patches which lacked feeding signs characteristic of uacaris using an area approximately 500 × 100 m adjacent to where feeding observations occurred; 17 such sites were found.

To test prediction 1 (easy escape route), distance from patch centre, of both exploited and unexploited patches, to nearest overhanging bough or other arboreal refuge, and distance to the nearest area of dense vegetation were measured (<4 m with tape measure, >4 m with laser rangefinder; Bushnell Corp., Overland Park, Kans., USA).

Prediction 2 (greatest seed density) was tested in two ways. First, 5 of the 17 sites lacking visual evidence for uacari seed predation were selected and, at these, information on seedling density and species composition were collected (chosen by using the first 5 novel numbers between 1 and 17 to appear in a table of random numbers). Mass and greatest dimension of seeds and proportional mass of seed versus seedling shoot (plumule) were also recorded. Second, we compared in-patch seedling density from the 17 unexploited and 7 exploited patches with the average seedling densities on unflooded igapó floor, using the number of seedlings and their species in 23 randomly placed 1 m² quadrats in unflooded igapó.

Prediction 3 (repeat visits) was investigated by examining feeding debris. Foraging uacaris ate only the seeds, biting off plumules and leaving them lying on the ground. The resulting wilting patterns were compared with experimentally cut-off plumules to provide a set of reference photos that allowed us to assess whether patches were visited once by uacaris or repeatedly, thus testing prediction 3 (repeat visits). Plumules were categorized as fresh (leaves unwilted or nearly so), wilted (2–3 days since bite: leaves green and supple but lacking luster), very wilted (4–6 days since bite: leaves dry and matt, pale green or grey) and indeterminate (clearly older than 6 days but too broken or dried out for certain classification).

Uacaris did not completely eat all seeds they removed from the seedling patches. Nor did they take to feeding perches some of the seedlings from which they had removed the plumules. To test the effects of partial seed consumption and plumule removal on viability, 25 seedlings from which the plumule had been removed and 25 bitten seeds were removed and replanted in soil collected at the site. Accompanied by 25 unbitten seeds (controls), these were placed in shaded individual plastic containers and watered naturally, when it rained. Survivorship was noted at 30, 60 and 90 days.

To calculate the mean mass of seedlings per square metre, the mean mass for each species was multiplied by the mean overall per square metre, corrected for the mean proportional representation of species present.

Analyses

Differences between the characteristics of patch types and between randomly placed quadrats and seedling patches were tested using 2-tailed Mann-Whitney U tests (significance level <0.005). For statistical significance in germination trials, Fisher's exact test (significance level $p < 0.005$) was used. To test if uacaris were preferentially selecting the seed of one species more than another, Ivlev's index of selectivity was calculated for each species by comparing the mean proportion of seeds eaten at all patches with their proportions in uneaten patches, using the formula:

$$I = (U - A)/(U + A)$$

where A is availability (proportion of total number in sample: eaten plus non-eaten) and U is use (eaten) [Ivlev, 1961]. A '0' Ivlev value indicates the species appears in the diet at the same frequency at which it occurs in the environment (i.e. no active selection). A value above 0 indicates positive selection, a negative value indicates avoidance.

Results

The material reported here is part of a larger study of *C. m. ouakary* feeding ecology at Jaú National Park [Barnett, 2010]. Overall, Barnett [2010] found only 10.5% (1,143 of 11,902) of feeding records and 11.7% of the time budget occurred in the lower strata of igapó, including the non-arboreal foraging reported here. The terrestrial feeding reported here represents a small part (7.7%) of all *C. m. ouakary* dry-season feeding records, but represents 100% of such feeding records in unflooded igapó, where no arboreal feeding was recorded, probably because there are no fruits or young leaves for uacari to forage upon at that time. Terrestrial feeding constituted 1.6% (190 of 11,902) of all feeding records, but represents over one third (37.5%) of all records of mature seed consumption for *C. m. ouakary*.

Feeding from Patches of Germinating Seeds – Behavioural Observations

All terrestrial feeding was observed between December 2007 and January 2008, during the brief period when the igapó forest was unflooded, and its floor was dry. On 6 separate occasions, groups of 2–5 uacaris ($n = 6$, mean 3.7 ± 1.36 SD) were observed feeding on germinating seedlings in open areas on the floor of unflooded igapó, and, at a seventh site, uacaris were disturbed while feeding on the ground, but left before observations could be made. An additional 2 sites were found where field signs (e.g. still moist lacerations on seed testas, plumules cut, but fresh and unwilted) showed feeding had occurred very recently. As uacaris have fission-fusion societies [Bowler and Bodmer, 2009], with groups of 40–100 animals commonly breaking into smaller groups to forage, it is likely that the observed animals were a foraging subgroup.

Uacaris were directly observed to eat 27 germinating seedlings of *Eschweilera tenuifolia* (Lecythidaceae), and 5 of an undetermined *Pouteria* species (Sapotaceae). An additional 191 partly eaten seeds were retrieved from patches where uacaris were seen feeding. These included at least 4 tree species (168 *E. tenuifolia*, 9 *Leopoldinia pulchra* (Arecaceae), 8 *Pouteria* sp. and 6 *Pouteria elegans*). Uacaris were seen to forage only in patches of germinating seeds, and no evidence of their seed feeding (such as bitten seeds or bitten-off plumules) was found away from seed patches, indicating they did not forage elsewhere for seeds on the forest floor. In igapó, seed patches are caused when floating seeds come to rest in rafts against obstructions such as floating branches, and so have a much higher density of seeds than in randomly selected areas of forest floor (see below).

Terrestrially foraging uacaris would eat 3 or 4 seeds from the seedlings at the patch, and then carry in their hands between 1 and 7 additional seedlings to eat at an arboreal refuge. This perch was always 1–4 m off the ground, with a good view of the surrounding forest floor. No member of a terrestrially foraging group was observed acting as sentinel, but individuals frequently broke off to scan upwards and horizontally. Quadrupedal movement was the most commonly observed, though

Table 1. Size and density of germinating seedlings at unexploited patches of similar sizes to patches at which feeding had occurred

Patch No.	Patch size, m ²	Seedlings, n	Seedlings (<i>E. tenuifolia</i> / <i>L. pulchra</i> / <i>P. elegans</i> / <i>Pouteria</i> sp.), %	Seedlings/m ²
1	1.8	536	97.1/1.9/0.9/0.1	297.8
2	2.2	1,307	91.8/2.1/3.9/2.2	594
3	2.6	743	84.5/8.1/4/3.4	285
4	3.0	1,246	80.1/11.1/5.9/2.9	415.3
5	3.5	1,026	98.9/0/0.4/0.7	292.3
Means ± SD	2.6 ± 0.66	971.6 ± 328.9	90.46 (± 8.04)/4.65 (± 4.72)/ 3.03 (± 2.31)/1.86 (± 1.41)	376.8 ± 132.7

uacaris heading to a perch would walk 3-limbed and carry seedlings in one hand. Bipedal hopping was also noted.

For all tree seeds eaten, uacaris ate only the seed, with plumules and young leaves being nipped off and discarded. Among the seedlings and plumules showing evidence of uacari seed predation were an additional 11 seedlings (3 *Eschweilera*, 8 *Pouteria*) with bite marks from rodent teeth. From their size (4–6 mm) and form, these were caused by *Dasyprocta* spp. Such seedlings did not have their plumules removed. The relative lack of rodent feeding records in *Eschweilera* patches was notable, especially as in the same area we recorded 43 incidences of rodent feeding on the cotyledons of *Swartzia acuminata* (Fabaceae) seedlings, 13 incidences of their feeding on fungi and 9 of their eating the inflorescences of the root parasite *Helosis cay-anensis* (Balenophoraceae).

The frequency at which *Eschweilera* seedlings were eaten by *C. m. ouakary* (88.9%) was nearly identical to the mean frequency in the 5 seed patches (90.5% ± 8.04, n = 5; tables 1, 2) where all seedlings (n = 4,858) could be counted and identified (Ivlev value, 0.0089). The other species were also eaten in proportions very similar to their abundance (Ivlev values of 0.085, 0.096 and 0.005 for *L. pulchra*, *P. elegans* and *Pouteria* sp., respectively; see table 1 for abundances). Hence, uacaris were not selecting *Eschweilera* seeds, but taking them in proportion to their absolute abundance.

Seed Germination Experiments

Of the 25 bitten seeds 100% had rotted by 90 days, as had 19/25 (76%) of seeds from which plumules had been removed. The other 6 showed no sign of new plumule production. Twenty (80%) of 25 unbitten seeds with intact plumules were still growing at 90 days. The difference between germination of damaged (n = 0/50) versus non-damaged seeds (n = 20/25) is significant (p < 0.0001, Fisher's exact test).

Characteristics of Germinating Seeds and Seed Patches

Of 24 large seedling patches investigated, uacaris fed at only 7. Patches at which feeding occurred were significantly closer to an off-the-ground refuge than those where no evidence of feeding was recorded (Mann-Whitney U test, 2-tailed, Z = 18.5,

Table 2. Areas of 7 patches of seedlings exploited by uacaris (patches No. 1–7), compared with 6 unexploited patches within 10 m of them (patches No. 8–13)

Patch No.	Patch size, m ²
Exploited patches	
1	1.6
2	2
3	2.2
4	2.4
5	2.8
6	3
7	3.8
Mean ± SD	2.54 ± 0.72
Unexploited patches	
8	0.4
9	0.6
10	0.8
11	1
12	1.1
13	1.6
Mean ± SD	0.91 ± 0.42

$p = 0.006$; means and SD, 2.6 ± 1.3 and 5.7 ± 2.7 m, respectively). Patches at which feeding occurred were also significantly further away from dense terrestrial vegetation than patches that lacked evidence of feeding (Mann-Whitney U test, 2-tailed, $Z = 17.5$, $p = 0.0083$; means and SD, 18.1 ± 4.9 and 12.5 ± 7.5 m, respectively; table 3).

On the igapó forest floor, the mean seedling density in 25 random 1 m² quadrats was 13.3 (SD ± 7.5 ; range 5–35; table 4). In contrast, mean seedling density in unexploited patches was 376.8/m² (SD ± 132.7 , $n = 5$; table 1). Used seedling patches had a mean area of 2.47 m² (SD ± 0.77 ; table 1), while the unused seedling patches used for calculating the density of seedlings and the mass of seedlings per patch had a mean area of 2.6 m² (SD ± 0.66 , $n = 5$). The areas of unvisited patches (table 1) were not significantly different from those at which feeding was observed (Mann-Whitney U test, 2-tailed, $Z = 0.405$, $p = 0.755$), indicating that the 5 unvisited patches could be validly used for estimating seedling densities at visited patches. Seedling mass varied between 11.6–24.9 g (mean 16.92, SD 4.87) for *E. tenuifolia* ($n = 13$) and between 35.4 and 48.9 g (mean 41.1, SD 16.14) for 4.9 g *P. elegans* ($n = 2$) with plumules making a small contribution to the overall mass (table 5). The total mass of seeds in a patch varied from 1,750 to 18,718 g (mean 14,460 g). Seedling density at unvisited seedling patches was significantly greater than typical seedling density on the forest floor (mean density of 13.3 seedlings/m²; table 4; Mann-Whitney U test, $Z = -3.462$, $p = 0.001$), hence the unvisited patches were used as a proxy for the density of the (now-density compromised) visited patches.

Foraging was not recorded in patches that were close to the used patch, but which were <1 m². Comparison of size of the visited and ignored patches showed uacaris were only recorded feeding in seed patches >2 m². Of the 17 unused patches of >1 m² that were studied, 6 were within 10 m of a visited patch. Patches at which uacaris fed were significantly larger than any of these 6, neighbouring but unused, patches (Mann-Whitney U test, 2-tailed, $Z = 2.857$, $p = 0.00427$; table 1).

Table 3. Distance to nearest arboreal refuge, and to dense terrestrial vegetation for feeding patches (1–7), and large ($\geq 1.5 \text{ m}^2$) uneaten patches (A–Q)

	Distance to nearest arboreal refuge, m	Distance to nearest dense terrestrial vegetation, m
Feeding patch		
1	0.5	21.5
2	1.8	19.3
3	3.4	18.6
4	4.2	15
5	3.6	17.9
6	2	25
7	2.6	9.2
Mean \pm SD	2.6 \pm 1.3	18.1 \pm 5
Non-feeding patch		
A	6	15
B	2	25
C	7	7
D	4.5	23
E	2.5	8
F	11	10
G	7	21
H	8	19
I	8.5	6
J	6	17
K	4.5	17
L	7.5	1
M	3.5	15
N	5	2
O	1.5	16
P	10	3
Q	4	7
Mean \pm SD	5.8 \pm 2.7	12.4 \pm 7.5

Fresh, wilted and very wilted nipped-off *Eschweilera* plumules were recovered from the same patch, indicating that patches were being used repeatedly. Comparison of the state of wilt of 100 plumules collected at feeding patches at which uacaris had fed with experimentally manipulated plumules, found fresh plumules (26%), plumules 2–3 days old (48%) and 4–6 days old (19%), with the remainder being indeterminate, as each wilt class suggests some measure of time since last feeding in a patch.

Then we assessed the mean mass of seedlings available per square metre. Excluding the uneaten (and probably toxic [Aparecida de Jesus, 2003; Mergalhães et al., 2003]) seedlings of *S. acuminata*, the mean percentile proportions of 90.5% *E. tenuifolia*, 4.6% *L. pulchra*, 3% *P. elegans* and 1.9% *Pouteria* sp. (table 1) were used. Using the mean value of 377 seedlings/m² (table 1), this gives 341 *E. tenuifolia*, 17 *L. pulchra*, 11 *P. elegans* and 7 *Pouteria* sp. seedlings per square metre. Multiplying by the mean

Table 4. Density and number of species of germinating seedlings in 1 m² quadrats on the floor of dry igapó forest

Quadrats	Seedlings/m ²	Species, n	<i>E. tenuifolia</i> , %
1	9	3	0
2	5	2	0
3	21	2	33.0
4	23	3	56.5
5	24	3	75.0
6	8	2	50.0
7	14	2	92.8
8	12	2	91.7
9	12	3	25.0
10	7	2	0
11	6	2	33.0
12	25	2	80.0
13	15	2	73.3
14	9	3	11.1
15	10	2	40.0
16	10	3	70.0
17	9	3	44.4
18	9	2	66.6
19	9	2	33.3
20	6	4	16.7
21	15	3	13.3
22	12	4	8.3
23	35	3	31.4
Mean ± SD	13.3 ± 7.52	2.6	41.1

Table 5. Mean size and mass of germinating seedlings encountered in patches

Species	n	Mean length ± SD mm	Mean mass ± SD g	Percent mass plumule
<i>E. tenuifolia</i>	13	60.03 ± 8.06	16.92 ± 4.87	1.5 ± 0.37
<i>L. pulchra</i>	10	21.16 ± 1.68	21.84 ± 3.42	3.57 ± 0.57
<i>P. elegans</i>	20	42.1 ± 7.05	41.15 ± 16.14	2.4 ± 0.8
<i>Pouteria</i> sp.	7	38.6 ± 6.5	32.6 ± 15.7	2.7 ± 0.8
<i>S. acuminata</i>	20	135.6 ± 26.72	239.5 ± 93.03	4.43 ± 1.23

masses for these seeds (table 5) gives 5,769.7 g of *E. tenuifolia*, 371.3 g of *L. pulchra*, 452.7 g of *P. elegans* and 228.2 g of *Pouteria* sp. seedlings per square metre. This gives a total of 6,821.2 g of edible seedlings per square metre. Exploited seedling patches had a mean size of 2.54 m², indicating a mass of 17,325.8 g of edible seedlings per mean patch.

Discussion

Our data supported prediction 1 (easy escape route), prediction 2 (greatest seed density/numbers) and prediction 3 (repeated visits). The study has shown seed patches at which *C. m. ouakary* fed were close to a refuge, were larger than those where no feeding was recorded and had high seedling densities. It appears highly likely that these patches were visited regularly. *C. m. ouakary* leaves a characteristic feeding signature, which is unlike that of either rodents or peccaries in the region. The differential stages of wilting observed in the discarded plant remains indicates repeat visits. This is interpreted as implying predator-sensitive foraging. Comparing this with actions by other *Cacajao* sp. is compromised by the lack of similar studies. Although white bald uacaris (*C. c. calvus*) were recorded foraging terrestrially for germinating seeds by Ayres [1986], associated foraging behaviour was not recorded and no information was provided on the dispersion of the seedlings. At Ayres' [1986] study site there was little terrestrial mammalian activity when the flooded forest was dry which led Ayres [1993] to suggest that terrestrial feeding occurred on the floor of unflooded várzea forest, primarily because it was a low-risk foraging strategy (see also Lopes and Ferrari [1994]). This was an appropriate explanation for várzea, where large predators are generally rare or absent from these broad flood plains [Bodmer et al., 1998; Haugaasen and Peres, 2005b], but is unlikely to be valid for the narrow ribbon-like igapó, as it is immediately adjacent to terra firme and is visited in the dry season by jaguar and other terra firme-based predators [Bodmer et al., 1998; Haugaasen and Peres, 2005b; Barnett, unpubl. data].

The study has shown that uacaris prefer large seed patches, distant from dense terrestrial vegetation and close to a source of arboreal refuge where most seeds were then eaten. We consider it plausible that uacaris are basing their decisions about where to forage on both density and quantity of germinating seeds and the risk involved in obtaining them. In addition, since the density of seeds in the grounded seed rafts far exceeded the density in other parts of the forest floor, we believe that uacaris also choose to feed on the most abundant terrestrial seed resource, the biomass of which is considerable. Whether uacaris cease to visit patches once seed densities fall below certain levels was not investigated in the current study, but is clearly an avenue for future research.

In the absence of information on relative predation rates on uacaris foraging at patches of different types, the interpretation that avoidance of seed patches near dense vegetation functions to reduce the possibility of predation is, of course, supposition. But, as Ferrari [2009] has pointed out, predation on primates may be rare precisely because of the predator avoidance strategies the animals employ. Such a strategy is, we believe, the most parsimonious interpretation of the available data. Terrestrially hunting predators known to take Neotropical primates include jaguar (*P. onca*) [Peetz et al., 1992; Olmos, 1994] and cougar (*P. concolor*) [Novack et al., 2005] preying on adults, and smaller felids preying on juveniles and infants [e.g. jaguarundi, *Puma yagouaroundi* [Tófoli et al., 2009]; ocelot, *Leopardus pardalis* [Miranda et al., 2005; Bianchi and Mendes, 2007]]. For the jaguar, ambush from dense vegetation is the most frequent hunting strategy [Seymour, 1989; Rosa and Nocke, 2000]. Foraging in várzea may be low risk because the floodplains on which they grow are extensive and consist of long, narrow, largely parallel levees;

consequently, connectivity to the predator-rich terra firme is low. In igapó, although foraging terrestrially may reduce the risk from aerial predators such as harpy eagles [Barnett et al., 2011], it is not a risk-free enterprise. Though most Amazonian mammals can swim [Goulding, 1990], floodwater seasonally prevents terrestrial mammals from foraging in igapó except for the 2–3 months when the waters recede and the forest floor is exposed. This period is one of intense germination activity [Parolin, 2001], and rodents, deer, tapir and peccary all enter into igapó to feed on this bonanza [Bodmer et al., 1998; Haugaasen and Peres, 2005a, b]. Predators, like jaguar and smaller cats, enter to feed on the herbivores [Seymour, 1989; Haugaasen and Peres, 2005b], as well as nesting river turtles and their eggs [Salera Jr. et al., 2009] and caiman eggs [Villamarín-Jurado and Suárez, 2009; Silveira et al., 2010].

With mean edible seedling mass per patch exceeding 17 kg, grounded seed rafts clearly represent a potentially important food resource for *C. m. ouakary*. However, in addition to abundance, food quality may also be an important factor in food choice. As seeds mature, their water content tends to decline, while the carbohydrate, fat and protein content proportionately increases [Laboriau, 1983]. Terrestrial foraging has not been reported for *C. m. melanocephalus* in Pico da Neblina, Brazil [Boubli, 1997], nor for *C. c. ucayalii* at Lago Preto, Peru [Bowler, 2007]. In both areas fruit is present year-round in the canopy, and this may well negate the need to descend to the ground to feed. This is not the case at Jaú, where the igapó forest has a marked seasonal fruit dearth [Barnett, 2010], such that there is little or no fruit or young leaves on which a uacari could forage.

We have shown that uacaris both remove seedlings and eat them and also that seeds bitten and then dropped seldom survive. This, and the fact that uacaris appear to repeatedly visit certain patches, means that they could be acting as sources of considerable seedling mortality within them. However, because the animals appear to be choosing patches where density is high, and also appear to prefer seeds that are just launching their plumules, it is considered very likely that uacaris will move to a second patch once the seedlings in the first become too old and sparse. Under such circumstances it is likely that these primates will, in fact, be acting as substantial thinning agents on the population of developing *Eschweilera* seedlings. Given the widely established effects of excessive crowding on seedling development and survivorship [Pacala and Silander, 1985, 1990; White, 1986], it is possible that uacaris are enhancing the survivorship possibilities of these seedlings which escape their attention. This possibility has also been mooted by Lopes and Ferrari [1994] for *C. c. calvus* and *Eschweilera albiflora*, though again the quantitative data to test it are lacking. However, similar effects have been recorded in other systems involving plants and mammalian seed predators. For example enhanced seedling mortality among *Berteroa incana* (Brassicaceae) plants in areas burrowed by pocket gophers (*Geomys bursarius*) also results in greater growth and survivorship among the non-predated seedlings [Reichmann, 1988].

Uacaris are not alone in foraging for seeds on the floor of igapó. Rodents, such as *Cuniculus*, *Dasyprocta* and *Proechimys* sp. are all known to enter and forage on seeds, though their foraging ecology in igapó is, to date, unstudied. From the very preliminary data, they appear to be slight competitors within the superabundant resource that each seed patch represents. In addition, we would argue that the foraging actions of the rodents themselves are of little or no functional importance to a forag-

ing uacari, which appears to be basing its decision to use a patch on the apparent size and density of the patch – and its proximity to escape routes and to potential predator-concealing cover – irrespective of the means by which such densities have been arrived at.

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