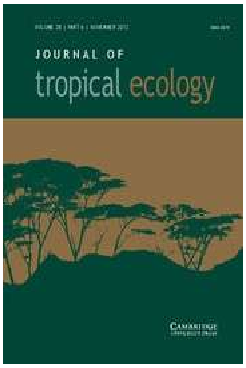

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Primary seed dispersal by three Neotropical seed-predating primates (*Cacajao melanocephalus ouakary*, *Chiropotes chiropotes* and *Chiropotes albinasus*)

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Abstract: The Neotropics house two guilds of large arboreal vertebrate seed predators: parrots and the pitheciin primates. Both have diets dominated by immature fruits. The possibility of members of the Pitheciinae (genera *Cacajao*, *Chiropotes* and *Pithecia*) acting as occasional seed dispersers has been mooted, but not experimentally shown. We combined primate behavioural data and seed germination data from three separate field studies in the Brazilian states of Amazonas and Pará to analyse patterns of post-consumption seed survivorship for seeds discarded by three pitheciin species (*Cacajao melanocephalus ouakary*, *Chiropotes chiropotes* and *Chiropotes albinasus*). We then calculated the frequency of dispersal events for four species eaten by *C. m. ouakary*. All three primate species dropped intact seeds while feeding, and 30.7% of 674 dropped seeds germinated ex situ. Undamaged seeds from unripe and ripe samples germinated (29.3% and 42.7%, respectively), and all three primate species carried some fruits up to 20 m from the parent tree before consuming them. Potential seed-dispersal events varied from 1 (*Macrolobium acaciifolium*) per fruiting cycle to more than 6500 (*Duroia velutina*), suggesting that there are differences in dispersal potential. In summary, although they are highly specialized seed predators, these primates may also act as important dispersers for some plant species, and effective dispersal is not restricted to ripe fruits, as immature fruits removed from a tree may continue to mature and the seeds later germinate, a much-neglected aspect of dispersal ecology. The possibility that similar events occur in parrots should be experimentally investigated.

Key Words: Amazonas, frugivore, primates, seed dispersal, seed predator

INTRODUCTION

Large-bodied (>3 kg), frugivorous primates are often important seed dispersers (Koné *et al.* 2008, Link & DiFiore 2006, Moses & Semple 2011, Poulsen *et al.* 2001, Stevenson *et al.* 2002). In such circumstances primates fit the criterion for true dispersal proposed by Howe (1989), in that as a result of dispersal (whether from expulsion in faeces, spitting out, being dropped during processing or carried to new locations: Lambert & Garber 1998), seeds are moved beyond the mother tree canopy. Primates are not tidy eaters, and it is common for a

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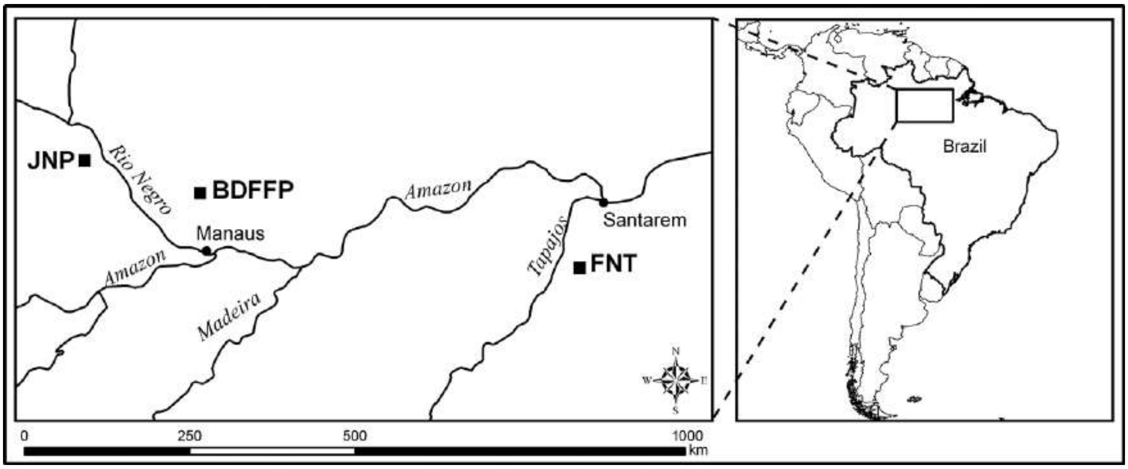

Figure 1. Study site locations for *Cacajao melanocephalus ouakary* (Jaú National Park; JNP); *Chiropotes chiropotes* (Biological Dynamics of Forest Fragments Project; BDFFP); and *Chiropotes albinasus* (Tapajós National Forest; FNP) in the Brazilian Amazon.

significant amount of food to be dropped during a feeding bout (de Figueiredo 1993, Zhang 1995). In frugivorous or granivorous species, many of these discarded items contain seeds.

Seed dispersal is considered a common byproduct of primate feeding, but such dispersal has not been regularly associated with three constituent genera (*Cacajao*, *Chiropotes* and *Pithecia*) of Neotropical primate subfamily Pitheciinae, all of which have traditionally been considered as specialist consumers of unripe seeds (Barnett & Brandon-Jones 1997, Barnett *et al.* 2005, Kinzey 1992). In species of uacari (*Cacajao* spp.) and cuxiú (*Chiropotes* spp.; also called bearded sakis, see Barnett *et al.* in press), seeds may exceed 60% of the diet (Ayres 1989, Boubli 1999, Boyle *et al.* 2012, Veiga 2006). Immature seeds dominate, and most are not ingested whole, but triturated to a pulp (Norconk 2011). Such primates are 'pre-dispersal seed predators' (sensu Janzen 1971). However, Norconk *et al.* (1998) considered the possibility that pitheciins can assist with seed dispersal via different mechanisms, including removing the pericarp and seed coat before dropping it and swallowing seeds without masticating them. However, these observations were not backed-up with germination trials. In another study, Grafton *et al.* (2002) found whole seeds of *Alibertia latifolia* and *Coccoloba striata* (Polygonaceae) in 83.1% of tested *P. pithecia* faecal samples (N = 160). However, this study also lacked germination trials and, while demonstrating dispersal was possible, did not conclusively demonstrate its occurrence.

Here we report on field studies of seed dispersal by three pitheciin seed-predators: the golden-backed uacari (*Cacajao melanocephalus ouakary*), the brown-backed cuxiú (*Chiropotes chiropotes*) and the red-nosed cuxiú (*Chiropotes albinasus*). The *Cacajao* population annually spends 9 mo (Barnett 2010) in blackwater flooded forest (igapó: sensu Prance 1979) and the two *Chiropotes* study populations inhabit lowland Amazonian unflooded (terra firme) forest (Boyle *et al.* 2009, Pinto 2008). Fruits of terra firme trees are mostly bird- or primate-dispersed, whereas fish and water are the dominant fruit dispersal agents in igapó (Correa *et al.* 2007, Goulding *et al.* 1988). Because of these fundamental disparities in dispersal ecology, we examined the potential for seed dispersal in igapó and terra firme species.

Uacaris and cuxiús are sclerocarpic foragers (Kinzey & Norconk 1990, Rosenberger 1992), specializing in hard-husked fruits whose protective pericarps they remove using their procumbent incisors and hypertrophied canines (Kinzey 1992). The eaten seeds are often immature, but, based on the work of Norconk *et al.* (1998), we hypothesized that these three species act as effective seed dispersers for some species. Therefore, we predicted that these three primate species may serve as primary dispersers of some plant species by (1) discarding or dislodging unripe and ripe fruit during feeding bouts, without damage to the seeds; (2) ingesting and subsequently defecating intact seeds; and (3) transporting the seeds from the mother tree; and that seeds under these three conditions would germinate successfully.

METHODS

The three pitheciin species were studied at three separate study sites in Brazilian Amazonia (Figure 1): *Cacajao melanocephalus ouakary* at Jaú National Park (Barnett *et al.* 2012b), *Chiropotes chiropotes* in forest fragments and continuous forest near Manaus (Boyle & Smith 2010, Boyle *et al.* 2009, 2012) and *Chiropotes albinasus* at Tapajós National Forest (Pinto 2008). These three studies were conducted independently and then the results brought together for comparative purposes of the current study. For this reason, differences exist in the precise details of how seed germination trials were conducted. However, we do not consider these variations to impair overall data comparability.

The Latin name for the golden-backed uacari follows Hershkovitz (1987) because the precise appellation is currently disputed (Boubli *et al.* 2008). *Chiropotes* taxonomy is also debated (Bonvicino *et al.* 2003, Hershkovitz 1985), and here we follow Barnett *et al.* (2012a, in press).

Study sites

Cacajao melanocephalus ouakary was studied in Jaú National Park (01°53.16′S, 61°44.31′W), a 2 227 000-ha protected area on the southern bank of the Rio Negro some 220 km upriver from Manaus, Brazil, between October 2006 and April 2008 (Barnett 2010). Data collection involved three groups of uacaris, two of which seasonally used both terra firme and igapó forests, and one of which used only igapó.

Chiropotes chiropotes was studied at the Biological Dynamics of Forest Fragments Project (BDFFP) site (02°20′S, 60°06′W–02°26′S, 59°44′W), approximately 60 km north of Manaus, from January 2005 until April 2006. During this time cuxiús were observed eating 244 plant species (Boyle *et al.* 2012). Data on seed dispersal, presented in this manuscript, were collected from January 2006 to April 2006. Data collection involved six groups, two that lived in continuous forest, two that lived in separate 10-ha forest fragments, and two that travelled between the continuous forest and two different 100-ha forest fragments.

Chiropotes albinasus was studied in Tapajós National Forest (FNT), Pará State, Brazil (03°21′S, 54°56′W), a 560 000-ha protected area approximately 100 km from Santarém on the Santarém-Cuiabá road, between August 2004 and January 2006 (Pinto 2008). Data collection involved a single group inhabiting an area of dense, little-disturbed, lowland rain forest.

Field protocols

At Jaú National Park, *C. m. ouakary* in igapó was followed either on foot or in paddled wooden canoes, depending on floodwater levels. Terra firme observations were made from two 2-km transects, walked at 1 km h^{-1}. Data on feeding and social behaviour were collected with scan sampling (Altmann 1974) every 30 s, in 5-min blocks, each block interspersed with 1-min of ad libitum sampling. At BDFFP, *C. chiropotes* groups were followed on foot (Boyle & Smith 2010, Boyle *et al.* 2012), with behavioural and ecological data recorded every 5 min using group scan sampling (Altmann 1974, Boyle & Smith 2010). At FNT three people independently walked a trail system covering 1400 ha, until one team member contacted the *C. albinasus* study group. The other two team members were then summoned by radio. Behaviour was recorded once per visible individual at 10-min intervals (Pinto 2008).

At all three sites, animals were searched for and observed, whenever possible, from the start of morning activity until the end of afternoon activity (*c.* 06h00–18h00). At all sites, samples of diet items were collected directly from beneath a feeding tree following a feeding bout. If supplemental material was required to aid identification, it was collected directly from feeding trees after monkeys had left.

For the golden-backed uacari and brown-backed cuxiú, plant material was identified using a field guide to fruits (van Roosmalen 1985), regional floras (Gentry 1993, Ribeiro *et al.* 1999), *Flora Neotropica* volumes and the herbarium staff at the National Institute for Amazonian Research (INPA), Manaus. For the red-nosed cuxiú, in addition to the above, a study site-specific field guide to trees (Parrota *et al.* 1995) was used, with specimen identities checked with Universidade Federal do Pará specialists.

Germination trials

In the *Cacajao* study, seeds that fell during feeding bouts were collected from seven locally abundant species: *Bombacopsis macrocalyx* (Bombacaceae), *Inga rhynchocalyx* (Fabaceae), *Macrolobium acaciifolium* (Fabaceae), *Eschweilera tenuifolia* (Lecythidaceae), *Eugenia* sp. (Myrtaceae), *Manilkara* sp. (Sapotaceae) and *Micropholis* sp. (Sapotaceae). These seven species were chosen with the criteria that their fruits were: (1) indehiscent and multi-seeded, or (2) dehiscent (either single or multi-seeded), plus were (3) zoochorous or hydrochorous, and (4) known to be eaten by uacaris. Species with indehiscent single-seeded fruits were excluded, since they would no longer function as dispersive propagules once fed-upon by uacaris, as the result would be either: (1) complete consumption, (2) embryo removal or (3) damage sufficient either to kill the seed outright or permit invasion of pathogens (i.e. testa breached). An eighth species, *Swartzia laevicarpa* Amshoff. (Fabaceae), was collected, but germination trials were terminated due to storm waters.

Igapó species were inundated prior to being tested for germination because fruits of these tree species frequently spend extended periods immersed before germination (Parolin 2000, 2001; Parolin *et al.* 2004). In a small forest stream near the research base, seeds were placed in plastic mesh bags and attached to immersed vegetation in a stream. Seeds were checked twice a month for 2 mo for signs of rot. Non-rotted seeds were then planted and monitored twice a month for 3 mo. For germination experiments, collected seeds were placed in plastic containers with forest-floor soil, then located in shade, covered in leaf litter and watered by natural rain showers. These studies were conducted at various times during the 19-mo residency at Jaú National Park, depending on when experimental subject species were fruiting. *Cacajao* faeces were also collected and analysed for the presence of seeds. In the field this analysis was done visually for large seeds and with a Beck portable dissecting microscope for smaller ones. The presence of very small seeds was assayed later in the laboratory using a Leica/WILD 3C binocular dissecting microscope, with a 10–40× zoom lens.

Separate inundation trials were conducted on *Licania heteromorpha* Benth. (Chrysobalanaceae) and *Swartzia acuminata* Willd. ex Vogel. (Fabaceae) in order to determine to what extent discarded items sink after being handled by the uacaris. For *L. heteromorpha*, 40 fruits had 25%, 50%, 75% or 100% of pericarp removed (10 fruits in each category), and then they were dropped from 1 m into igapó water, and given 30 s to surface and float. The same procedure was followed with *S. acuminata*, except these 40 fruits had 20%, 30%, 40% or 50% of the pericarp removed.

For both *Chiropotes* species, the exigencies of the behavioural study meant it was not possible to monitor seedlings in situ beneath parent trees. Hence, in the *C. chiropotes* study, seed germination was studied ex situ. All fruit items discarded during feeding were recorded over 4 mo (January–April 2006) of the 16-mo field project, and each classified for: ripeness (ripe, unripe), part eaten (fruit and/or seeds), and part(s) discarded (intact fruit, partially intact fruit, seed only). These items were collected and transported to the BDFFP base in Manaus. Here, under netted shade, seeds were placed in individual potting-soil filled plastic containers, watered regularly and monitored monthly for germination until December 2006. Germination was recorded as successful if the seed germinated and the seedling then remained alive for the duration of the study. Faeces were collected during daily follows and subsequently placed in soil and treated as above. Ex situ germination greatly diminishes the possibility of seed and seedling mortality by such biotic agents as seed-predating beetles, peccaries and fungi, so the resultant germination percentages may therefore overestimate the potential of *C. chiropotes* as a seed disperser.

For the *C. albinasus* study at FNT, germination experiments were not conducted. Field observations were, however, made on whether dropped items were ripe or unripe, whether fruit and/or seeds were eaten, and the parts discarded (defined as: intact fruit, partially intact fruit, seed only).

Frequency of dispersal

To be considered a legitimate disperser (Bustamente *et al.* 1992), an animal species must not only be capable of dispersing a plant species, but do so regularly. We investigated pitheciin potential to act as legitimate dispersers by calculating the maximum possible number of dispersal events for which an animal could be responsible. The full dataset required to calculate dispersal events was only available for *C. m. ouakary*. We collated the mean number of fruits *C. m. ouakary* ate daily for four species: *Duroia velutina* Hook f. ex K. Schum (Rubiaceae), *Eschweilera tenuifolia* (Lecythidaceae), *Inga rhynchocalyx* (Fabaceae) and *Macrolobium acaciifolium* (Fabaceae). We then multiplied this number by the mean seed number in each fruit (data derived from our own studies and van Roosmalen 1985). To obtain the number of seeds potentially dispersed, we then multiplied this figure by the number of days fruiting (from our phenological studies), and then divided this maximum number by 23% (the percentage that Norconk *et al.* 1998 recorded of fruits being dropped with pericarp removed). To get the maximum number of possible dispersal events, we then divided seeds potentially dispersed the value the percentage germination recorded for each of the four studied species (Table 1).

RESULTS

All three pitheciin species dropped seeds from intact and partially intact fruit to the ground while feeding (Figure 2), and all three species consumed seeds from unripe and ripe fruit. *Cacajao m. ouakary* ate fruits and seeds from 111 species: 95 species (85.6%) for their unripe seeds, 10 (9%) for ripe seeds, 10 (9%) for pulp, and six (4.5%) for arils or sarcotestas (nine (8.1%) appeared in more than one category). Of these 111 species, 33 (29.7%) were either multi-seeded and/or hydrochorous. When feeding on *Eschweilera tenuifolia*, in 31 of 33 (93.9%) of the observations, *C. m. ouakary* removed less than one dozen seeds (approximately 70 seeds or more were in each pyxidium) before the remainder tumbled into the water. While feeding on *Bombacopsis macrocalyx*, the uacaris extracted one to five unripe seeds; of 50 just-jettisoned fruits, 39 (78.0%) had at least one seed remaining.

During the *C. chiropotes* germination study (January–April 2006), the monkeys discarded items during feeding from 84 individual trees and lianas from 49 species (35 genera, 20 families: Appendix 2), and 33.2% of the discarded items had at least one intact seed remaining.

Table 1. Maximum potential number of seed dispersal events per individual monkey per fruiting cycle for four plant species eaten by *Cacajao melanocephalus ouakary* at Jaú National Park, Amazonas, Brazil. Used the 23.5% figure from Norconk *et al.* (1998) to calculate both the proportion of single-seeded fruits dropped, and the number of fruits dropped per feeding on multi-seeded fruits. † Indicates aril removed by *C. m. ouakary*.

Plant species	Mean no. fruit seen eaten daily	Mean ± SE (N) no. seeds	Fruiting period (d)	No. seeds potentially dispersed	Germination (%)	Maximum no. potential dispersal events
Duroia velutina	0.35	280 ± 106 (10)	120	11 760	56	6586
Eschweilera tenuifolia	3.7	37 ± 16.7 (43)	90	12 321	8 (unripe)	986
					42 (ripe)	5175
Inga rhynchocalyx	0.13	6.1 ± 1.7 (10)	30	23.8	68†	16
Macrolobium acaciifolium	0.03	1 ± 0 (25)	90	3	30	1

Of the 84 trees and lianas, 63% were consumed for unripe seeds, 35% for ripe seeds, 29% for pulp, arils and sarcotestas, and 2% were unknown (percentages total more than 100% because some species had multiple parts consumed).

Chiropotes albinasus was recorded consuming 125 plant species from 38 families. These cuxiús ate mature fruits of 62 species in 32 families (Appendix 3), the most important being: *Moutabea guianensis* (Polygalaceae: 13.5%, N = 274 feeding records), *Pouteria bilocularis* (Sapotaceae: 13%) and *Goupia glabra* (Goupiaceae: 12.4%). Of the 62 species eaten in the mature state, 51 (82.3%) were eaten only for their pulp, with the ripe seeds either swallowed whole (30 species, including *Abuta panurensis*: Menispermaceae), or discarded (six species, including *Caryocar glabrum*: Caryocaraceae).

Incidences of dispersal

Germination from ripe and unripe fruit. Germination success was not uniform across plant species, but it did occur in 30.7% of the pooled data (*C. m. ouakary*: 26.4% of 276 seeds germinated within 3 mo; *C. chiropotes*: 32.7% of 398 seeds germinated within 6 mo, and 24.9% germinated within 2 mo). In the *C. m. ouakary* study, the 73 germinating seeds came from seven species (seven genera, five families); all seven species were consumed for their seeds (Appendix 1). In the *C. chiropotes* study, the 130 germinating seeds came from 36 individual plants, which represented 26 species (19 genera, 14 families); 16.7% were consumed for their fruit only, 11.1% for their fruit and seeds, and 72.2% for their seeds only (Appendix 2). Germination did not occur in any of the seeds that had been damaged (partially masticated) by the monkeys.

Examining the pooled data, germination occurred in 29.3% and 42.7% of the undamaged seeds from unripe and ripe fruit, respectively. In the *C. m. ouakary* study, 17.9% of the 67 seeds from unripe fruit germinated (two of four species had some germination), and 55.0% of 111 seeds from ripe fruit germinated (all six species had some germination). In the *C. chiropotes* study, 32.9% of 216 seeds from unripe fruit germinated (13 of 31 species had some germination), and 34.7% of 170 seeds

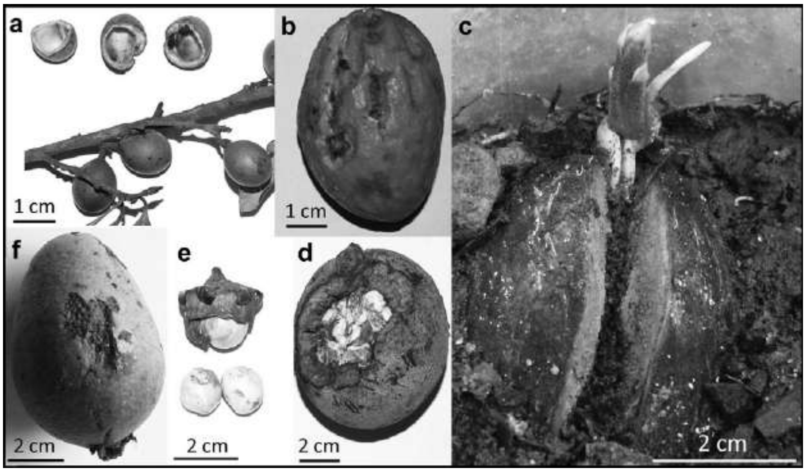

Figure 2. Intact fruits and seeds that were dropped by *Chiropotes chiropotes* and subsequently germinated within 6 mo: *Pouteria* sp. (Sapotaceae) fruits (a); *Catostemma albuquerquei* (Bombacaceae) seed with partial removal of pericarp by a monkey (b); *C. albuquerquei* seed germinating 7 wk later (c); *Caryocar villosum* (Caryocaraceae) fruit with seed partially exposed (d); *Eschweilera truncata* (Lecythidaceae) seeds (e); and *Couepia longipendula* (Chrysobalanaceae) fruit (f). Photo credits: Sarah Boyle.

from ripe fruit germinated (14 of 26 species had some germination). Germination of seeds from unripe and ripe fruits was significantly different for the *C. m. ouakary* data ($\chi^2 = 23.7$, df = 1, $P < 0.001$), but not for the *C. chiropotes* data ($\chi^2 = 0.14$, df = 1, $P = 0.71$).

Impacts of handling on the fruits. Although partially masticated seeds did not germinate, removal of the pericarp or sarcotesta did not negatively impact germination in terra firme habitats. *Chiropotes chiropotes* fully removed the pericarp from 19.3% of the 398 seeds that were dropped, and partially removed the pericarp from 35.9% seeds. Germination success was greatest in seeds with no remaining pericarp (41, 53.2%), followed by seeds with intact pericarp (64, 36.0%), and seeds with partially removed pericarp (25, 17.5%); these differences in germination success were significant ($\chi^2 = 30$, df = 2, $P < 0.001$). A comparison of *Inga rhynchocalyx* seeds dropped during *C. m. ouakary* feeding bouts found that ex situ 17 of 21 (81.0%) of sarcotesta-less seeds from under the *C. m. ouakary* feeding tree germinated, while 23 of 25 (92%) of sarcotesta-retaining seeds died from fungal infection within 7 d. Although it was not directly observed, it appeared that the uacaris sucked away the sarcotesta and then spat out the seeds.

In igapó habitat, the removal of aril or pericarp impacts the buoyancy of the seeds. *Cacajao m. ouakary* opened *Swarzia laevicarpa*, removed the aril, and jettisoned the seed and pericarp. These seeds sank; however, of the nine immersed seeds that were part of the inundation trials, 100% were unrotted after 60 d. Although *C. m. ouakary* ate only the aril of *Swarzia acuminata*, jettisoning the pericarp and seed; 4 of 23 (17.3%) seeds that were jettisoned by the monkeys had so little pericarp remaining that the seeds immediately sank. Buoyancy trials found 100% of *S. acuminata* seeds sank when $\geq$ 40% of the pericarp was removed. With *Licania heteromorpha*, *C. m. ouakary* scraped off the pulp with its incisors in 13 of 41 (32%) behavioral observations. Of these 13 items, 9 (69%) had 50–95% of the pulp removed. Buoyancy trials found that seeds sank when >25% of the pulp was removed.

Faeces. Seeds were found in the faeces of all three primate species, but at overall low quantities. In *C. m. ouakary*, 37 of 146 (25%) of faecal pellets contained whole *Duroia velutina* seeds. In germination trials with 19 of these seeds, 74% germinated. There was no difference in germination success between seeds that had passed through the digestive system of *C. m. ouakary* and seeds that had not be consumed by the monkeys ($\chi^2 = 0.53$, df = 1, $P = 0.47$). No other seeds were found intact in *C. m. ouakary* faeces. Nineteen faecal samples from *C. chiropotes* had small fragments of seeds, plus very small intact seeds. When placed in soil none of these seeds germinated during the subsequent 3–6 mo. Few *C. albinasus* faecal pellets were encountered, but the majority of these contained intact seeds of *Abuta panurensis* (Menispermaceae), *Brosimum* sp. (Moraceae) and two species of Sapotaceae.

Distances from the parent tree. All three primate species at times moved from the parent tree to eat the fruit or seed. In 97 of the 183 (53%) times *C. m. ouakary* was seen feeding on *E. tenuifolia*, the monkeys moved away from the feeding tree with the opened pyxidium in hand, feeding on it up to 20 m from the original tree. For *Inga rhynchocalyx*, *C. m. ouakary* fed from one location where broken pods with seeds retaining their sarcotesta were found in the leaf litter, as well as seeds lacking sarcotestas. The seeds lacking sarcotestas were found up to 30 m away from the feeding location. In 65% of the feeding events on *Caryocar villosum* (Caryocaraceae), *C. chiropotes* carried the fruits 20–30 m to a new tree, where some or all of the pericarp was removed, and the seed dropped. As with both *C. m. ouakary* and *C. chiropotes*, *C. albinasus* commonly carried fruits for tens of metres from the parent tree before eating the fruits. The wind-dispersed *Couratari guianensis* and *C. stellata* were opened by *C. albinasus* by being battered against tree trunks until the lid of the pyxidium broke away, and seeds became accessible. Mature *Couratari* seeds are light, and frequently large quantities of them were carried by the wind while *C. albinasus* handled them.

Frequency of dispersal. The potential number of seed dispersal events by *C. m. ouakary* during a fruiting cycle was large for *Duroia velutina* (6586 events, potentially 11 760 seeds dispersed) and *Eschweilera tenuifolia* (6161 events, potentially 12 321 seeds dispersed), though much less for *Inga rhynchocalyx* (16 events, potentially 68 seeds dispersed) and *Macrolobium acaciifolium* (1 event, potentially 3 seeds dispersed; Table 1).

DISCUSSION

We consider it likely that three pitheciin species (*C. m. ouakary*, *C. chiropotes* and *C. albinasus*) that have been deemed primarily as seed predators, may be considered 'effective seed dispersers' (Schupp 1993, Schupp *et al.* 2010), at least for some plant species. We found evidence that these primates routinely drop intact seeds to the ground while feeding, and that such seeds, if they have not been damaged during processing or mastication, can germinate successfully. All three species fed upon unripe and ripe seeds and fruit, and undamaged seeds from both ripe and unripe fruit germinated. In fact, germination success with terra firme species was greatest when the monkeys had removed the pericarp or aril. Furthermore, the three primate species appear to assist with dispersal by dropping seeds away from the parent tree. Some intact seeds were found in the faeces, and germination was successful with *Duroia velutina* in *C. m. ouakary* faeces; however, due to the low occurrence of seeds in the faeces, we do not consider faeces to be the prime mode of dispersal for these three pitheciins.

More than 200 seeds from 23 genera germinated after being dropped by *C. m. ouakary* and *C. chiropotes* (Appendices 1, 2, respectively), suggesting that the potential for pitheciins to assist with seed dispersal is not trivial. Although the *C. albinasus* study did not conduct germination trials, behavioural data suggest that this species may also aid in seed dispersal, especially of larger, multi-seeded fruits. The number of seeds that were dropped by the monkeys and later germinated could be great for one individual tree: e.g. one *Castostemma albuquerquei* tree had 15 of its large seeds dropped by *C. chiropotes* during 3 d of observations of these monkeys in January 2006. All 15 of the seeds germinated in 2–10 mo (mean: 3.7 mo). In addition, *C. chiropotes* dropped seeds from 84 individual plants, and seeds from 43% of these plants germinated. Such seeds may also be available to terrestrial secondary seed dispersers earlier than if they were to fall from the parent tree without aid from primates.

Germination was not restricted to ripe fruits, as immature fruits removed from a tree may continue to mature and the seeds later germinate, a much-neglected aspect of dispersal ecology. There was no difference in per cent of seeds that germinated from unripe and ripe fruit for the *C. chiropotes* data, but seeds from ripe fruit had significantly greater success than seeds from unripe fruit for the *C. m. ouakary* data. We think that the different findings may be attributed to sample size, as only four plant species were represented in the *C. m. ouakary* study for unripe fruits. Although it would be great to examine more species in the future, we think that the findings that seeds from unripe fruit can later germinate after being dropped by the monkeys, are important to understanding dispersal ecology.

Mastication of the seeds does appear to damage the seeds, as none of the damaged seeds germinated. We consider it notable that damage broke the testa (thus facilitating pathogen ingress) and did not simply scarify it (as reported by Janzen 1971 for tapir). Furthermore, removal of the pericarp or aril by the monkeys did not negatively impact germination in terra firme species, suggesting that pericarp removal does not always prejudice seed germination possibilities: consequently, pitheciins could disperse such seeds. In addition, fungus infested nearly all *I. rhynchocalyx* seeds from which the sarcotesta was not removed. In igapó species, it is important that the natural buoyancy of viable seeds or fruits is not compromised, permitting natural germination. The dispersal of hydrochorous species may be limited if the primates remove substantial amounts of pulp.

Seeds that are ingested but not masticated sufficiently to kill them can germinate if expelled in faeces, as supported by germination of *Duroia velutina* seeds from *C. m. ouakary* faecal pellets. Some seed fragments were found in *C. chiropotes* faeces, and though none germinated in the experimental time period, a positive result might have occurred with more time, as some tropical species require extended periods to germinate (Vázquez-Yanes & Orozco-Segovia 1993). Intact seeds of *Abuta panurensis* (Menispermaceae), *Brosimum* sp. (Moraceae), and two Sapotaceae species were found in *C. albinasus* faeces. Although jettisoned seeds and faecal pellets were not collected in the *C. albinasus* study, these observations indicate that the potential exists for *C. albinasus* to disperse seeds. Overall, seed dispersal via faeces can occur, but its occurrence in pitheciins may not be great.

Primates commonly feed while moving, accounting, for example, for up to 18.4% of monthly feeding activity of *C. m. ouakary* (Barnett 2010). All three pitheciine primates frequently moved to a different site to eat a plucked fruit (e.g. 73% of all *C. m. ouakary* feeding events on *E. tenuifolia* and 65% of all *C. chiropotes* feeding events on *Caryocar villosum*, of which 14% of the collected seeds germinated). In *Inga rhynchocalyx*, seeds that were spat out were found at greater mean distances from the parent tree than were seeds that had not been handled by the monkeys. Such actions may be significant in igapó where floating fruits suffer substantial levels of predation (Correa *et al.* 2007, Kubitzki & Ziburski 1994). In igapó, dehiscent species, such as *Eschweilera tenuifolia*, risk predation from freshwater chelonia (Pérez-Emán & Paolillo 1997), and large frugivorous/granivorous fish such as *Collosoma macropomum* G. Cuvier (Characidae), *Heros* spp. (Cichlidae) and doradid catfish (Doradidae), whose molariform teeth crush seeds (Correa *et al.* 2007, Goulding *et al.* 1988). Such predation is greatest when fruits/seeds are dropping below a parent tree: *C. macropomum*, for example, hold station beneath such trees for several days, consuming many hundreds of seeds during the period (Araújo-Lima & Goulding 1998, Goulding *et al.* 1988). Clearly, *C. m. ouakary* feeding movements could potentially move seeds beyond such predator concentrations. Both *Chiropotes* species may also assist with dispersal by providing tapirs and terrestrial rodents with seeds which they secondarily disperse (Adler 1995, Galetti *et al.* 2001, Jorge & Peres 2005), while avoiding not only large seed predators such as peccaries which often gather under fruiting trees (De Steven & Putz 1984), but also bruchid beetles and other density-dependent micro-predators (Rios & Pacheco 2006, Salm 2006).

Although pitheciins are likely to assist with some seed dispersal, it seems unlikely that any plant species has strong dispersal links to them. For example, during fieldwork at Jaú National Park, a variety of mammals (*Cebus albifrons* Humboldt (Cebidae), *Saimiri sciurieus* Linnaeus (Cebidae), *Eira barbara* Linnaeus (Mustelidae)), and birds (*Amazonas festiva* Linnaeus (Psittacidae), *Brotogeris sanctithomae* Müller (Psittacidae), *Pionites melanocephala* Linnaeus (Psittacidae)) were observed consuming the pulp of *D. velutina*: and seed-containing remnants falling to the water were eaten by fish and chelonia. Consequently, *C. m. ouakary* may be but one in a suite of vertebrate dispersers for this common riverside understorey tree. It is also possible that pitheciins reduce the potential of superior dispersers to be attracted to the tree, thereby increasing the cost to the tree and potentially decreasing its fitness.

In summary, it seems that, because the primates studied here regularly triturate ingested seeds rather than swallowing them whole, neither *Cacajao* nor *Chiropotes* will have as extensive or important a seed disperser role as those Neotropical primates which ingest and excrete complete seeds (e.g. *Alouatta*, *Ateles*, *Lagothrix* species: Chaves *et al.* 2010, Julliot 1997, Stevenson *et al.* 2002). However, the simple calculations presented in Table 1 yield impressively high values for potential dispersal events by *C. m. ouakary*. While post-germination mortality (which can be substantial, Chambers & MacMahon 1994, Vallejo-Marín *et al.* 2006) would doubtless diminish the numbers substantially, these pitheciins commonly travel in groups of up to 40 animals in the fruiting sessions of the species considered (Barnett 2010, Boyle *et al.* 2009), consequently a single group has substantial potential for seed dispersion at the local level.

Our observation that immature pitheciin-dispersed seeds germinated after being separated from the parent plant is an important one; although such maturation has been recorded elsewhere (Butler *et al.* 2009, Fenner & Thompson 2004), it appears to have been an overlooked possibility when analysing pitheciin seed-disperser potential. Clearly, this capacity greatly enhances the potential of these immature seed predators as seed dispersers.

The data presented here are preliminary. The key observation is that, even within species as highly morphologically specialized for seed predation as the three analysed here, viable and regular dispersal of seeds does occur. Therefore the potential for pitheciins as seed dispersers may be greater than we originally thought. The predictions of Norconk *et al.* (1998) are supported: species of both *Cacajao* and *Chiropotes*, as seed-predating primates, can (and do) disperse seeds.

Future studies should investigate whether secondary dispersers move discarded fruit, to what distance, to what extent the seeds germinate in the field, and the extent of subsequent mortality. The relevance of these results to parrots and squirrels should also be considered, as both are predators of mature and immature seeds (parrots: Berg *et al.* 2007, Galetti 1997, Renton 2006, Simão *et al.*1997; squirrels: Heaney 1978, Paschoal 1995). Given the potential demonstrated in the current study for immature seeds to mature and subsequently germinate away from the parent tree, the roles of squirrels and parrots may also have to be revised and considered, at least partially, to serve as dispersers, for some species.

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Appendix 1. Taxonomy and germination success for seven plant species consumed and dropped by *Cacajao melanocephalus ouakary* during feeding bouts at Jaú National Park, Amazonas, Brazil. The part eaten was categorized as seed (S), fruit (F), unripe (U), ripe (R) or unknown (UN). Seeds that fell during feeding were classified as unripe or ripe, and intact or non-intact (partially masticated by a monkey). *Indicates sarcotesta consumed instead of the entire seed.

		Germinated seeds/total seeds (%)			
Plant species	Part eaten	Unripe, intact	Unripe, non-intact	Ripe, intact	Ripe, non-intact
Bombacopsis macrocalyx (Ducke) A. Robyns (Bombacaceae)	S (U)	7/9 (77.8)	n/a	n/a	n/a
Inga rhynchocalyx Sandwith (Fabaceae)	S (R)*	n/a	n/a	17/21 (81.0)	n/a
Macrolobium acaciifolium (Benth.) Benth. (Fabaceae)	S (U)	n/a	0/19 (0.0)	6/20 (30.0)	0/17 (0.0)
Eschweilera tenuifolia (O. Berg) Miers (Lecythidaceae)	S (U)	0/25 (0.0)	n/a	13/25 (52.0)	0/11 (0.0)
Eugenia sp. (Myrtaceae)	S (R)	0/10 (0.0)	0/7 (0.0)	4/10 (40.0)	n/a
Manilkara sp. (Sapotaceae)	S (U)	n/a	0/10 (0.0)	8/10 (80.0)	0/9 (0.0)
Micropholis sp. (Sapotaceae)	S (U)	5/23 (21.7)	0/25 (0.0)	13/25 (52.0)	n/a

Appendix 2. Taxonomy and germination success for a sample of plants consumed by *Chiropotes chiropotes* at the Biological Dynamics of Forest Fragments Project, Amazonas, Brazil. The part eaten was categorized as seed (S), fruit (F), unripe (U), ripe (R) or unknown (UN). *Indicates sarcotesta consumed instead of the entire seed. A full list of the 244 plant species consumed is available in Boyle *et al.* (2012).

Plant species	Part eaten	Germinated seeds/ total seeds (%)	Mean time (mo) until germin-ation	N Indiv.plants from which seeds came
Anisophyllea manausensis Pires & W.A. Rodrigues (Anisophylleaceae)	S (U)	0/4 (0.0)	n/a	1
Duguetia stelechantha (Diels) R.E.Fr. (Annonaceae)	F (R)	0/8 (0.0)	n/a	1
Castostemma albuquerquei Paula. (Bombacaceae)	F (R)	15/16 (93.8)	3.7	2
Caryocar villosum (Aubl.) Pers. (Caryocaraceae)	F (R)	2/14 (14.3)	9.0	1
Pourouma cucura Standl. & Cuatrec. (Cecropiaceae)	S (U)	0/13 (0.0)	n/a	1
Pourouma tomentosa Miq. (Cecropiaceae)	F (R)	1/1 (100.0)	2.0	1
Couepia longipendula Pilg. (Chrysobalanaceae)	S (U)	1/3 (33.3)	1.0	2
Couepia sp. (Chrysobalanaceae)	S (U)	0/2 (0.0)	n/a	1
Licania longistyla (Hook. f.) Fritsch (Chrysobalanaceae)	UN	0/4 (0.0)	n/a	1
Clusia insignis Mart. (Clusiaceae)	S (U)	16/21 (76.2)	1.8	1
Clusia panapanari (Aubl.) Choisy (Clusiaceae)	S and F (R)	0/4 (0.0)	n/a	1
Moronobea coccinea Aubl. (Clusiaceae)	S (R)	0/3 (0.0)	n/a	1
Duckeodendron cestroides Kuhlm. (Duckeodendraceae)	F (U)	1/4 (25.0)	8.0	1
Croton lanjouwensis Jabl. (Euphorbiaceae)	S (U)	1/7 (14.3)	4.0	1
	S (R)	0/7 (0.0)	n/a	1
Hevea guianensis Aublet. (Euphorbiaceae)	S (U)	0/1 (0.0)	n/a	1
Abarema cochleata (Willd.) Barneby & J.W.Grimes (Fabaceae)	S (U)	0/9 (0.0)	n/a	2
Derris amazonica Killip (Fabaceae)	S (R)	3/4 (75.0)	1.0	3
Hymenaea parvifolia Huber (Fabaceae)	S (R)	1/1 (100.0)	2.0	1
Inga rubiginosa (Rich.) DC. (Fabaceae)	S (R)*	9/23 (39.1)	1.3	1
Inga sp. (Fabaceae)	S (U)*	0/3 (0.0)	n/a	1
Macrolobium limbatum Spruce ex Benth. (Fabaceae)	S (U)	0/5 (0.0)	n/a	2
Swartzia cuspidata Spruce ex Benth. (Fabaceae)	S (U)	0/2 (0.0)	n/a	1
Cheiloclinium sp. (Hippocrateaceae)	S (R)	0/1 (0.0)	n/a	1
	S (U)	0/4 (0.0)	n/a	2
Salacia insignis A. C. Sm.(Hippocrateaceae)	S (R)	0/1 (0.0)	n/a	1
	S (U)	0/4 (0.0)	n/a	2
Eschweilera cyathiformis Mori (Lecythidaceae)	S (U)	3/6 (50.0)	1.0	1
Eschweilera truncata A.C. Sm. (Lecythidaceae)	S (R)	0/1 (0.0)	n/a	1
	S (U)	9/20 (45.0)	1.4	8
Lecythis prancei S.A. Mori (Lecythidaceae)	S (U)	0/3 (0.0)	n/a	1
Strychnos cogens Benth. (Loganiaceae)	S and F (R)	1/6 (16.7)	3.0	2
Abuta sp. (Menispermaceae)	S (U)	1/1 (100.0)	6.0	1
	F (R)	0/2 (0.0)	n/a	1
Telitoxicum minutiflorum (Diels) Moldenke (Menispermaceae)	S (U)	0/1 (0.0)	n/a	1
Helicostylis tomentosa Poepp. & Endl. (Myristicaceae)	F (R)	0/4 (0.0)	n/a	1
Osteophloeum platyspermum (A.DC.) Warb. (Myristicaceae)	S (U)	2/27 (7.4)	1.0	4
Moutabea guianensis Aubl. (Polygalaceae)	S (U)	3/7 (42.9)	4.7	1
Malanea sp. (Polygalaceae)	F (R)	0/16 (0.0)	n/a	1
Chrysophyllum sanguinolentum (Pierre) Baehni (Sapotaceae)	S (R)	1/3 (33.3)	1.0	1
Chrysophyllum wilsonii T.D. Penn. (Sapotaceae)	S (U)	0/1 (0.0)	n/a	1
Ecclinusa guianensis (Caucho) Eyma (Sapotaceae)	S (U)	0/6 (0.0)	n/a	2
Manilkara bidentata (A.DC.) A.Chev. (Sapotaceae)	S and F (R)	17/17 (100.0)	2.5	4
Manilkara cavalcantei Pires & Rodrigues ex T.D. Penn (Sapotaceae)	S (R)	0/3 (0.0)	n/a	1
Manilkara huberi Chevalier (Sapotaceae)	S (U)	0/1 (0.0)	n/a	1
Pouteria anomala (Pires) T.D. Penn. (Sapotaceae)	S and F (R)	1/2 (50.0)	2.0	2
Pouteria erythrochrysa T.D. Penn. (Sapotaceae)	S and F (R)	1/1 (100.0)	1	1
Pouteria filipes Eyma (Sapotaceae)	S (U)	0/2 (0.0)	n/a	1
	S (R)	1/7 (14.3)	1.0	1
Pouteria freitasii T.D. Penn. (Sapotaceae)	S and F (R)	3/4 (75.0)	2.0	1
Pouteria guianensis Aubl. (Sapotaceae)	S (R)	4/6 (66.7)	2.0	1
Pouteria hispida Emya (Sapotaceae)	S (U)	1/3 (33.3)	2.0	1
Pouteria vernicosa T.D. Penn. (Sapotaceae)	S (U)	0/1 (0.0)	n/a	1
Pouteria virescens Baehni (Sapotaceae)	S (U)	0/2 (0.0)	n/a	1
Pouteria sp. (Sapotaceae)	S (U)	28/42 (66.7)	1.7	4
	S (R)	0/16 (0.0)	n/a	1
Sarcaulus brasiliensis (A.DC.) Eyma (Sapotaceae)	S (U)	4/4 (100.0)	1.3	1
Qualea labouriauna Mart. (Sapotaceae)	S (U)	0/6 (0.0)	n/a	1

Appendix 3. Taxonomy and treatment of mature fruit recorded in the diet of *Chiropotes albinasus* at Tapajós National Forest, Pará, Brazil, during 11 mo between August 2004 and January 2006 (n = 38 complete days).

Plant species	How seeds treated	Mature fruits	Feeding records (%)
Anacardium spruceanum Benth, ex. Engl. (Anacardiaceae)	–	10	0.19
Bocageopsis sp. (Annonaceae)	Ingested	9	0.17
Heteropsis sp. (Araceae)		3	0.06
Philodendron megalophyllum Schott. (Araceae)		2	0.04
Protium punticulatum Macbr. (Burseraceae)	Ingested	6	0.12
Caryocar glabrum (Caryocaraceae)	Discarded	58	1.12
Pourouma guianensis Aubl. (Cecropiaceae)		31	0.60
Pourouma tomentosa (Cecropiaceae)	Discarded	4	0.08
Licania sp. 2 (Chrysobalanaceae)		6	0.12
Clusia grandiflora Splitg. (Clusiaceae)		4	0.08
Tovomita sp. (Clusiaceae)	Ingested	11	0.21
Rourea krukovii Steyerm. (Connaraceae)		20	0.38
Dicranostyles sp. (Convolvulaceae)		24	0.46
Tetracera willdenowiana Steud. (Dilleniaceae)	Ingested	68	1.31
Sloanea sp. (Elaeocarpaceae)		3	0.06
Glycydendron amazonicum Ducke (Glícia) (Euphorbiaceae)		1	0.02
Hymenaea parvifolia Huber (Fabaceae)	Some ingested, some discarded	109	2.10
Inga alba (Sw.) Willd. (Fabaceae)	Ingested	40	0.77
Inga capitata Desv. (Fabaceae)	Ingested	15	0.29
Inga heterophylla Willd. (Fabaceae)	Ingested	24	0.46
Dipteryx odorata (Aubl.) Willd. (Fabaceae)	Discarded	6	0.12
Laetia procera (Poepp. & Endl.) Eichler (Flacortiaceae)	Ingested	32	0.62
Goupia glabra Aubl. (Goupiaceae)		253	4.87
Endopleura uchi (Huber) Cuatrec. (Humiriaceae)	Discarded	19	0.37
cf. *Phoradendron* (Loranthaceae)	Ingested	15	0.29
Abuta panurensis Eichler (Menispermaceae)	Ingested	146	2.81
Brosimum guianense (Aubl.) Huber (Moraceae)	Ingested	8	0.15
Brosimum lactescens (S. Moore) C.C. Berg (Moraceae)	Ingested	14	0.27
Brosimum parinarioides Ducke (Moraceae)	Ingested	58	1.12
Ficus mathewsii (Miq.) Miq. (Moraceae)	Ingested	1	0.02
Pseudolmedia laevis Macbr. (Moraceae)		24	0.46
Iryanthera sagotiana (Benth.) Warb. (Myristicaceae)		13	0.25
Virola sp. (Myristicaceae)		10	0.19
Eugenia patrisii Vahl. (Myrtaceae)		20	0.38
Eugenia sp. 2 (Myrtaceae)		1	0.02
Minquartia guianensis Aubl. (Olacaceae)	Discarded	18	0.35
Passiflora acuminata DC (Passifloraceae)	Ingested	5	0.10
Moutabea guianensis Aubl. (Polygalaceae)	Ingested	274	5.27
Paullinia sp. 1 (Sapindaceae)	Ingested	44	0.85
Paullinia sp. 2 (Sapindaceae)	Ingested	43	0.83
Vouarana sp. (Sapindaceae)		2	0.04
Chrysophyllum sp. 1 (Sapotaceae)	Ingested	8	0.15
Chrysophyllum sp. 2 (Sapotaceae)	Ingested	4	0.08
Manilkara huberi (Sapotaceae)		1	0.02
Manilkara paraensis (Huber) Standl. (Sapotaceae)		10	0.19
Micropholis venulosa (Mart. & Eichl.) Pierre (Sapotaceae)	Ingested	39	0.75
Pouteria bilocularis (H. Winkl.) Baehni (Sapotaceae)	Ingested	265	5.10
Pouteria macrophylla (A.DC.) Eyma (Sapotaceae)		10	0.19
Pouteria manaosensis (Aubrév. & Pellegr.) T. D. Penn. (Sapotaceae)	Ingested	10	0.19
Pouteria sp. 1 (Sapotaceae)	Ingested	11	0.21
Pouteria sp. 2 (Sapotaceae)	Ingested	87	1.67
Pradosia sp. 1 (Sapotaceae)	Ingested	50	0.96
Sarcaulus brasiliensis (Sapotaceae)	Ingested	4	0.08
sp. 1 (Sapotaceae)		13	0.25
Solanum sendtnerianum Van Heurck and Müll. Arg. (Solanaceae)	Ingested	5	0.10
Apeiba echinata Gaertn. (Tiliaceae)		7	0.13
sp. 1 (Unidentified Tree)		22	0.42
sp. 4 (Unidentified Tree)		6	0.12
sp. 3 (Undetermined Plant)		8	0.15
sp. 4 (Undetermined Plant)		8	0.15
sp. 5 (Undetermined Plant)	Ingested	8	0.15
sp. 6 (Undetermined Plant)	Ingested	7	0.13