

Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: consequences for seed dispersal effectiveness

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Abstract: Primates are primary seed dispersers for many tropical tree species. Different species of primates vary considerably in ranging and feeding behaviour, seed processing, and in seed defecation patterns. Here we compare the role of two arboreal primate species, howlers (*Alouatta palliata*), and white-faced monkeys (*Cebus capucinus*) as seed dispersers in a tropical dry forest in Costa Rica. We found that *Cebus* produce smaller defecations, spend shorter times feeding per tree, have longer seed dispersal distances, and produce a more scattered pattern of seed deposition in the forest than *Alouatta*. In addition, *Cebus* moved more frequently between trees, and consumed fruits of more species than *Alouatta*. We examined the consequences of the contrasting defecation patterns produced by *Cebus* and *Alouatta* on the early seed fate of *Acacia collinsii*. We found that quantity, but not the identity (*Cebus* vs. *Alouatta*) of faecal material affected post-dispersal activity. Seeds in scattered faeces, sufficiently apart from each other (the common defecation pattern of white-faced monkeys), had higher short-term survival than seeds in clumped patterns of faeces (the pattern associated with *Alouatta*).

Key Words: *Acacia collinsii*, *Alouatta palliata*, *Cebus capucinus*, Costa Rica, defecation patterns, dispersal effectiveness, post-dispersal, primates, seed dispersal, seed removal, tropical dry forest

INTRODUCTION

Seed dispersal has a direct effect on the distribution of individuals within populations and on the colonization of new habitats, which in turn affects the rates of gene flow and the genetic structure of plant populations (Dirzo & Domínguez 1986, Hamrick *et al.* 1993, Martínez-Ramos & Soto-Castro 1993, Schupp 1988). Seed dispersal is also involved in the dynamics of forest regeneration and therefore in the long-term maintenance of plant communities (Lambert & Garber 1998, Webb & Peart 2001). Given the relevance of the dispersal process many people have tried to disentangle the complex phenomena occurring between the production of a seed and the establishment of a new plant (Jordano & Schupp 2000). In many instances frugivorous animals mediate this process, and consequently the ultimate fate of seeds

depends on the effectiveness of the frugivores consuming them.

The effectiveness of a frugivorous species as a seed disperser has been defined as the contribution it makes to plant fitness (Fleming *et al.* 1993, Schupp 1993). Effectiveness in turn depends on the quantity of seeds dispersed and on the quality of dispersal provided to each seed (Herrera *et al.* 1994, Jordano & Schupp 2000, Schupp 1993). As pointed out by Chapman (1989) and Schupp (1993), while much emphasis has been given to the quantity component, the quality component of seed dispersal (such as the location and pattern of seed deposition) may be the single most important factor determining the final fate of a seed (Janzen 1982a, 1986; Schupp 1993, Zhang & Wang 1995).

The quality component of dispersal includes fruit handling, seed treatment, dispersal distance and the type of site where the seed is deposited. Once a seed is deposited, the probabilities of germination and establishment depend on the physical environment and on the likelihood of encountering post-dispersal seed predators and secondary dispersers. Characteristics of the

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faecal material surrounding dispersed seeds may strongly influence these probabilities. Faecal matter modifies the local environment of seeds, altering moisture and nutrient supply (Coughenour & Detling 1986), and can be used as a visual or olfactory cue by seed predators (Andresen 1999, Chapman 1989, Howe 1989, Janzen 1982a, b; Rowell & Mitchell 1991, Zhang & Wang 1995). It is therefore possible that differences in dispersal effectiveness among frugivorous species are related, at least partially, to differences in their patterns of defecation (Andresen 1999, Zhang & Wang 1995).

In neotropical forests, Chapman (1989) and Julliot (1996a) reported the important role played by *Ateles geoffroyi* (Kuhl 1820), *Alouatta palliata* (Gray 1849), and *Cebus capucinus* (Linnaeus 1758) as seed dispersers. *Cebus* and *Alouatta* constitute between 25 and 40% of the frugivore biomass in the tropical forests they inhabit (Chapman 1995, Eisenberg & Thorington 1973) and consume and disperse large quantities of fruits and seeds (Chapman 1995, Estrada & Coates-Estrada 1984, Rowell & Mitchell 1991). Different species of primates may differ in their dispersal effectiveness depending on their behaviour, physiology, morphology and defecation patterns (Howe 1989, Janzen 1983b, Levey 1987, Lieberman & Lieberman 1986, Poulsen *et al.* 2002, Zhang & Wang 1995).

In this study we characterized the seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata* (hereafter *Cebus* and *Alouatta*, respectively), and experimentally evaluated the consequences of the faecal material on the short-term survival of *Acacia collinsii* Saff. seeds, a common small tree (up to 5 m) at our study site. Both species of primate inhabit the same area in a tropical dry forest of Costa Rica and differ greatly in terms of behaviour, physiology and morphology. We first made a general characterization of *Cebus* and *Alouatta* as seed dispersers. Because the quality component of dispersal could fluctuate if animals exploit resources that are unevenly distributed in time and space (like most fruiting trees), we explored how some attributes like diet, and seed dispersal distances vary in space and time. Our previous observations indicate that *Cebus* monkeys tend to defecate individually in space and time creating a scatter of small defecations. In contrast, troops of *Alouatta* defecate simultaneously at the same place producing large areas of clumped defecations. We evaluated this spatial pattern of droppings generated by the two species. Based on our preliminary data and on studies revealing an important effect of faecal quantity on seed survival (Andresen 2002, Janzen 1982a, 1986; Zhang & Wang 1995), we hypothesized that because high quantity of faecal material constitutes a major stimulus (visual or olfactory) for seed predators, seed survival in *Cebus* faeces should be higher than in *Alouatta* faeces. This hypothesis was evaluated by means of a field

experiment simulating the natural droppings of *Cebus* and *Alouatta*.

METHODS

Study site

This study was conducted in the Palo Verde National Park, Costa Rica (10° 21' N, 85° 21' W). The site is described by Tosi (1969) and Vaughan *et al.* (1982). Palo Verde is about 20 000 ha and includes several ecosystems such as tropical dry deciduous forest, evergreen forest, seasonal swamp and marshes. The climate is characterized by a marked dry season from mid-December to the end of May. Mean annual rainfall is 1500–2000 mm.

Study species

The black howler monkey, *Alouatta palliata*, is one of the largest primates in Central and South America, with a body mass ranging from 7–9 kg. Troop sizes lie in the range 3–26 individuals and overall mean densities estimated in Palo Verde were 69 individuals km⁻² (Massey 1987). Diet consists mainly of leaves but it also eats fruits (Estrada & Coates-Estrada 1984, 1986; Glander 1975, Massey 1987, Milton *et al.* 1980).

Cebus capucinus ranges from Honduras to Ecuador (Wolfheim 1983) and is a relatively small primate with a body mass ranging from 2–3.5 kg (Milton 1984). It consumes fruit, but also vertebrates, shoots, eggs and invertebrates (Milton 1984, Mitchell 1989, Moscow & Vaughan 1987, Oppenheimer 1968). Troop sizes at Palo Verde vary between 15 and 23 individuals (Massey 1987, Moscow & Vaughan 1987), with overall mean densities of 15 individuals km⁻² (Massey 1987).

Feeding, movements, and distribution of faeces

To describe the foraging behaviour and dispersal characteristics of the two primate species, two groups of *Alouatta* (group L: 8 individuals; group J: 10 individuals), and two of *Cebus* (group P: 16 individuals; group R: 22 individuals) were followed for a total of 47 d throughout the study (dry season: April–July 2000, *Cebus*: 14 d, *Alouatta*: 10 d; wet season: July–September 1999, *Cebus*: 11 d, *Alouatta*: 12 d). Our observations began at sunrise (06h30) when monkeys were leaving their sleeping sites, or at any time after finding the group, and finished at sunset (18h00) when they stopped in trees to sleep. Seeds handled by monkeys were categorized as spat out, damaged, and swallowed. Whenever possible, every tree used as a fruit source was identified to the species level.

Different attributes of the seed dispersal provided by *Cebus* and *Alouatta* such as the time spent eating in fruiting trees, and the dispersal distances were evaluated. We used the Mann–Whitney U-test to evaluate the differences in time spent eating in fruiting trees between monkey species. We used an Analysis of Variance to test the effect of species of monkey, season and the interaction on the number of species h^{-1} and fruiting trees h^{-1} visited. Faecal samples were collected from the forest floor or from understorey vegetation while following the monkeys. These samples were taken to the laboratory and all seeds were separated from faeces, counted, measured, and identified to species. Seeds < 1 mm long were not counted, and their numbers in faeces were estimated within categories (few: 20–50, many: 50–100, numerous: > 100 seeds). When available from faeces, a sample of 10–40 seeds was used to test viability. We distinguished, mapped, and counted all droppings reaching the forest floor. We calculated the distances between nearest-neighbour droppings. Thus, by grouping number of droppings within each class of distance, we obtained a simple measure of dispersion for both species of monkey. We tested differences in the frequency of faeces deposited at different distances between the two monkey species using the χ^2 test. Seed dispersal distances depend on the average time of passage through the digestive tract and on the distance travelled since the seeds were consumed. The daily distances travelled by the troops, the position of all trees used as food sources, and all the locations where defecations were deposited were estimated by using a GPS (Garmin 12), compass and pedometer. We used these measurements, along with estimations of the average time of passage of seeds throughout the guts of monkeys, to estimate mean seed dispersal distances. The straight-line distances between trees and the position of the group after seed retention time were calculated directly on maps. Mean seed retention times through *Cebus* (1.40 h, range 0.75–3 h) and *Alouatta* (18 h, range 16–25 h) digestive tracts were obtained from studies with captive monkeys (*C. capucinus*, Wehncke *et al.* 2003; and *A. palliata*, Estrada & Coates-Estrada 1984, Julliot 1996a, b; Milton *et al.* 1980).

Effect of defecation patterns and faecal identity on seed removal

To assess whether the quantity of faecal material and the identity of faeces influence post-dispersal seed removal, we performed a field experiment during the dry season of 2000. We simulated the contrasting patterns of defecation by using a factorial design with quantity (three levels; 0, 5 and 50 g of faeces) and identity (two levels; *Alouatta* and *Cebus*) of faecal material as factors, and evaluated the effects of these treatments on the

seed removal of *Acacia collinsii*. *Acacia collinsii* fruits are legumes with an edible sweet pulp. On the one hand, this experiment required that a high number of seeds could be available and on the other, we are interested in the consequences of the faecal material on post-dispersal seed removal. We used this species because of its high availability of seeds and because they are actively sought by rodents (Wehncke and Numa, pers. obs.). Each treatment consisted of 10 *A. collinsii* seeds (average size: 0.54 ± 0.08 cm, $n = 20$) embedded in the surface of the assigned amount and type of faecal material. Controls consisted of 10 seeds without faecal material. We used 10 seeds because this approximates to the maximum number of seeds of this species found in a single dropping of *Cebus* and to the average number of seeds in these ranges of size found in a single dropping of *Alouatta*. Only fresh faecal samples (no older than 1 d) and mature seeds were used in the experimental treatments. Faecal samples were collected from the field and kept at 4 °C, and all the original seeds were removed before the experiment. Twenty replicates of each treatment were randomly distributed along a transect in the forest. Treatments were placed at least 25 m apart from each other. To have a qualitative estimate of the proportion of sites with rodent visitation, we recorded rodent activity by daily censuses of footprints on sand beds that were set around our experimental sites. Because our main interest was to evaluate the effect of faecal material as a visual or olfactory cue to seed predators, and given that faeces were completely dry after the third day, our censuses were restricted to a 5-d period. We assumed that it is during this period when the influence of faeces is maximum. The effect of the amount and identity of faecal material on seed removal was evaluated by means of a proportional hazard survival model (Fox 1990, Muenchow 1986). This procedure is a semi-parametric regression model that analyses the effect of explanatory variables on survival times (SAS Institute 1995), and produces a Likelihood-Ratio test that approximates to a Chi-square test (Fox 1993). Statistical analyses were performed using the computer software JMP 3.1. (SAS Institute 1995).

RESULTS

Feeding, movements and distribution of faeces

Cebus and *Alouatta* differed in seed handling (Appendix I). During the study period, *Cebus* and *Alouatta* consumed a total of 33 and 10 species of fruits, respectively (Appendix II). *Cebus* defecated a greater percentage of faecal samples containing seeds (*Cebus*: 98%, $n = 162$; *Alouatta*: 54%, $n = 68$). While *Cebus* swallowed seeds of

up to 1.5 cm long (although those > 0.9 cm were commonly spat out), *Alouatta* swallowed seeds of up to 2.4 cm. Most of the seeds in the faeces of both species were found intact. From approximately 4200 seeds from different species found in *Cebus* faeces, only 20 seeds of two species were found destroyed. We found no damaged seeds in *Alouatta* faeces. *Cebus* spent less time feeding per fruiting tree than *Alouatta* (median = 10 min, $n = 119$ for *Cebus*; median = 20 min, $n = 23$ for *Alouatta*, Mann–Whitney $U = 14$, $P = 0.0002$). Of the three factors evaluated only the species of monkey yielded significant results. *Cebus* visited more fruiting trees (median = 1 tree h^{-1} , $n = 22$ for *Cebus*; median = 0.3 trees h^{-1} , $n = 8$ for *Alouatta*, Mann–Whitney $U = -2.2$, $P = 0.03$) and species h^{-1} than *Alouatta* (median = 0.8 species h^{-1} , $n = 22$ for *Cebus*; median = 0.2 species h^{-1} , $n = 8$ for *Alouatta*, Mann–Whitney $U = -2.5$, $P = 0.01$).

In general, the distances travelled by monkeys in 1 d tended to be approximately straight lines. Mean seed dispersal distances produced by *Cebus* were significantly different between seasons (154 ± 121 m, $n = 48$ and 210 ± 160 m, $n = 45$, for wet and dry seasons, respectively, Median test = 27, $P < 0.05$). *Cebus* are very mobile animals; the highest probability (0.45) of movement away from trees was recorded in the first 10 min, less than the mean seed transit time through their gut (100 min, Wehncke *et al.* 2003), in other words, before defecation. We do not have this kind of data for *Alouatta* because during this study fruit-eating events were very scarce.

There were only 8 out of 81 observations in which more than one individual of *Cebus* defecated simultaneously in space. In contrast, almost all individuals of a group of *Alouatta* defecated simultaneously in space before moving to the next feeding tree (33 observations), thus creating areas of defecation. When a dropping of *Alouatta* dung reached the floor, most neighbouring faeces were deposited within 1–5 m (67% of their faeces), creating areas of high concentration of faeces and seeds (Figure 1a). In contrast, *Cebus* deposited 50% of their faeces at distances > 10 m from each other (Figure 1b). *Cebus* and *Alouatta* differ significantly in the distribution of faeces deposited at different distances ($\chi^2 = 12.4$, $P < 0.05$).

Effect of seed dispersal patterns and faecal identity on seed removal

The proportional hazards model showed no effect of the identity of faecal material on the probability of seed removal ($\chi^2 = 0.04$, $df = 1$, $P = 0.844$; Figure 2a). In contrast, the quantity of faecal material had a marked and significant effect on the probability of seed removal ($\chi^2 = 44.6$, $df = 2$, $P < 0.0001$; Figure 2b). Seeds in

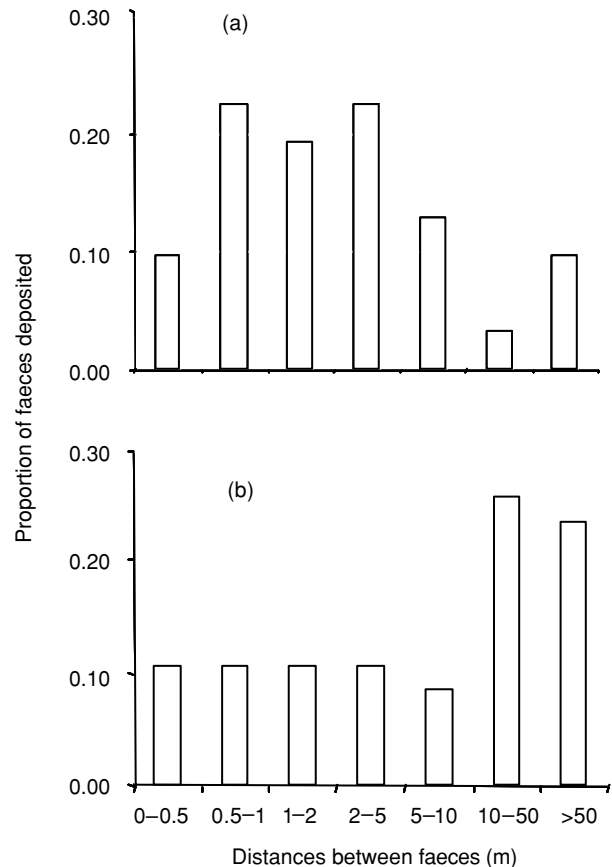


Figure 1. Proportion of faeces deposited by *Alouatta* (a) and *Cebus* (b) at different ranges of distances; $n = 31$ and 47 for *Alouatta* and *Cebus*, respectively.

relatively large amounts of faeces had a lower median life expectancy than seeds in the low-quantity treatment. These differences were attributable to the 50-g treatment ($\chi^2 = 7.22$, $P = 0.007$), because the 5-g treatment was not significantly different from control (no faeces) ($\chi^2 = 0.36$, $P = 0.55$). The interaction between quantity and identity of faeces was not significant ($\chi^2 = 3.37$, $df = 2$, $P = 0.19$). From daily censuses of footprints on sand beds we found that rodents visited more than 80% of sites.

DISCUSSION

Seed dispersal by white-faced and howler monkeys

The two species of primate studied here can be considered 'opportunistic' or 'non-restricted' frugivores because fruits do not represent the main bulk of their diet. It has been hypothesized that non-restricted frugivores, as a group, produce similar ecological and evolutionary

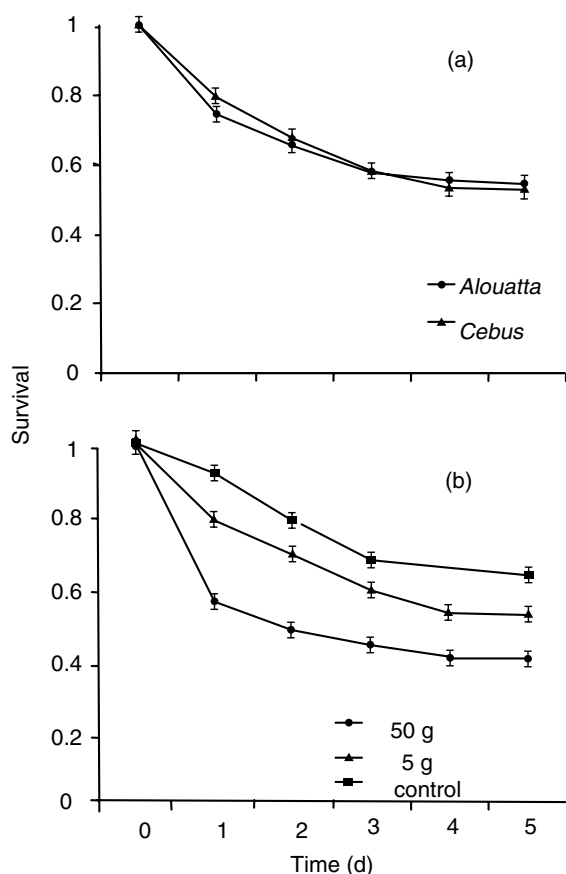


Figure 2. Survival curves for seeds of *A. collinsii*, according to the type of faeces (a) and quantities of faeces (b). Control = no faeces. Bars are standard errors of the life-table estimate. All curves end at census date.

consequences for the fitness of plants, and quite different consequences if compared with restricted frugivores (Fleming *et al.* 1993, Howe 1993). Here we showed that the short-term ecological consequences for seeds swallowed by two non-restricted frugivores can be completely different. Both *Alouatta* and *Cebus* play an important role as seed dispersers for many tree species in tropical dry forests (Chapman 1989). However, as revealed by this study, there are many aspects in which the dispersal services they provide differ. The contrasting defecation patterns of *Alouatta* and *Cebus* are the result of the different dietary strategies of these two monkey species (feeding behaviour, digestive physiology), and these patterns have a marked effect on the short-term survival of dispersed seeds. Although one of the commonly established requirements for considering a seed dispersal agent as effective is the quantity of seeds dispersed (Chapman & Onderdonk 1998, Stevenson 2000), the quality of seed dispersal may change the final fate of seeds (Schupp 2002).

Alouatta live in cohesive groups that commonly use fruiting trees that offer crops large enough to feed the whole troop, and spend a relatively long time resting in trees. Before moving to another tree, all or most of the individuals defecate more-or-less simultaneously, and this behaviour occurs approximately twice a day. Thus, they produce high amounts of faeces per defecation area (> 250 g inside an area of 2–5 m in diameter). Because of their slow digestive rate, 60% of defecations of a focal troop occur under their sleeping sites (Chapman 1989, Howe 1980, Julliot 1997). Therefore, it is very common that *Alouatta* concentrate high numbers of seeds under their main sleeping sites (Julliot 1996a, 1997). Reported mean dispersal distances of *Alouatta* range between 94–262 m (Estrada & Coates-Estrada 1984, Julliot 1996a, 1997). On the other hand, the feeding groups of *Cebus* (the number of animals feeding in a same tree) vary in size (10–15 individuals per troop), and social relationships inside the group determine which and how many individuals can feed in a tree at the same time (Janson 1990a, b). This forces subordinate individuals to forage on trees with small crop sizes, thus increasing the number of dispersed plant species. As a result, *Cebus* have a broad diet, spend a short time in each tree and travel about 4 km d⁻¹, moving seeds appreciable distances away from the parent plant and depositing them in a scattered pattern. Compared with other sympatric primate species, *Cebus* has short gut retention times (*A. palliata*: 20.4 h, *Ateles geoffroyi*: 4.4 h, *Cebus* sp.: 1.7 h) (Milton 1984, Wehncke *et al.* 2003). This results in higher rates of defecation per day and fewer seeds per faeces.

Effect of seed dispersal patterns and faecal characteristics on seed removal

Results from our experiment showed that the amount of dung is an important factor in determining the short-term removal of seeds and are in accordance with the results of Andresen (2002) and Zhang & Wang (1995). Seeds embedded in relative large quantities of faeces had a higher probability of removal than seeds in small quantities and without faeces. We are confident that most of the seed removal we observed may be attributed to rodents. Dung beetles were not active during the study period (dry season) (Janzen 1983a), and rodent activity was frequently recorded in all the experimental sites (footprints in sand beds placed around experimental sites; E. W. and C. N., pers. obs.). Janzen (1971) and Zhang & Wang (1995) pointed out that seeds removed by terrestrial rodents often represent seed predation, particularly when resources are scarce. In another study, Forget *et al.* (2002) through an annually based model for hoarding in neotropical forests, stated that during the period of

low availability of fruit, predation surpasses hoarding (ratio hoarding/predation < 1). Consequently, we think that all the *A. collinsii* seeds that were removed in this experiment were destroyed. This result is in accordance with other studies that have shown that rodents are attracted to sites with relatively high concentrations of faecal material (Andresen 1999, 2001; Chapman 1989, Estrada & Coates-Estrada 1991, Janzen 1982a, Shepherd & Chapman 1998). However, we cannot disregard the possibility that some seeds could escape predation and survive in the seed bank after secondary dispersal.

Seeds in the small quantity of faeces and control treatments had a 38% increase in their short-term survival in comparison with seeds in the large-quantity treatment. This result suggests that a scattered pattern of defecation of small quantities of faeces produce the better conditions for the short-term survival of dispersed seeds. It also underlines the importance of the quality component of seed dispersal and that of the patterns of defecation produced by different dispersers. Nonetheless, our results contrast with those of Andresen (2002), since she concluded that seeds embedded in relatively large quantities of faeces had higher probabilities of seedling establishment than those in small amounts of dung. Large dung piles attracted more dung beetles, which in turn collected and buried more seeds from these piles than from smaller ones. However, because Andresen (2002) did not report the probability of predation associated with the amount of dung, and since she evaluated the effects of rodents and dung beetles in independent experiments, it is not possible to determine whether or not the positive effect of dung beetles overcomes the negative effect of rodents.

Our results indicate that the variation in the defecation patterns produced by different primate species may play an important role in determining seed fate. Furthermore, the discrepancy between the results of Andresen (2002) and ours highlights the dynamic nature of the seed dispersal process. Finally, it is worth mentioning that the dispersal quality provided by any given animal is not constant, but could depend on the particular ecological scenario where dispersal occurs.

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Appendix I. Principal fruit species in the diet of *Cebus capucinus* and *Alouatta palliata*, during the study. Overlap in food plants by the two species of monkey = 30%.

Family	Species	Seed handling		Seed defecated	
		<i>Alouatta</i>	<i>Cebus</i>	<i>Alouatta</i>	<i>Cebus</i>
Anacardiaceae	<i>Spondias mombin</i>	sw	sp	i	no
Anacardiaceae	<i>Spondias purpurea</i>	sw	sp	i	no
Apocynaceae	<i>Stemmadenia obovata</i>	sw	sw	no	i
Boraginaceae	<i>Cordia dentata</i>	sw	sw	i	i
Bromeliaceae	<i>Bromelia pinguin</i>	no	sw	no	i
Burseraceae	<i>Bursera simaruba</i>	no	dr	no	no
Capparidaceae	<i>Capparis baducca</i>	no	sw	no	i
Capparidaceae	<i>Capparis indica</i>	no	sw	no	i
Cucurbitaceae	<i>Cayaponia attenuata</i>	no	sw	no	nd
Ebenaceae	<i>Diospyros nicaraguensis</i>	no	sw	no	i
Flacourtiaceae	<i>Casearia tremula</i>	no	sw	no	i
Fabaceae/Mimos	<i>Samanea saman</i>	sw	sp	i	no
Fabaceae/Mimos	<i>Acacia collinsii</i>	no	sw	no	i
Fabaceae/Mimos	<i>Pithecellobium oblongum</i>	no	sw	no	i
Meliaceae	<i>Trichilia martiana</i>	no	sw	no	i
Minispermaceae	<i>Hyperbaena tonduzii</i>	no	sw	no	i
Moraceae	<i>Brosimum alicastrum</i>	sw	sp	i	no
Moraceae	<i>Maclura tinctoria</i>	sw	sw	i	i
Moraceae	<i>Ficus nitida</i>	sw	sw	i	i
Moraceae	<i>Ficus cotinifolia</i>	sw	sw	i	i
Olacaceae	<i>Ximenia americana</i>	no	sw	no	i
Passifloraceae	<i>Passiflora platyloba</i>	no	sw	no	i
Piperaceae	<i>Piper tuberculatum</i>	no	sw	no	i
Polygonaceae	<i>Coccoloba</i> sp.	no	sw	no	i
Rubiaceae	<i>Guettarda macrosperma</i>	no	sp	no	no
Sapindaceae	<i>Paullinia pinnata</i>	no	sw	no	i
Sapindaceae	<i>Allophylus occidentalis</i>	no	sw	no	i
Tiliaceae	<i>Muntingia calabura</i>	no	sw	no	i
Viscaceae	<i>Phoradendron dipterum</i>	no	sw	no	i
Vitaceae	<i>Cissus alata</i>	no	sw	no	i

sw, swallowed; sp, spat out; dr, dropped; i, intact; nd, no data; no, not consumed. For botanical nomenclature see Chavarría *et al.* (2001).

APPENDIX II

Fruit and seed characteristics of the principal species in the diet of *Cebus capucinus* and *Alouatta palliata*, during the study.

Spondias mombin (yellow ellipsoid drupe 1.5–3.5 cm, single seed 2.4 ± 0.45 cm), *Spondias purpurea* (red ellipsoid drupe 2.6 cm, single seed 2.1 ± 0.1 cm), *Stemmadenia obovata* (green round capsule 7–10 cm, orange aril, numerous seeds 0.8 ± 0.09 cm), *Cordia dentata* (white round fleshy drupe > 1 cm, single seed 1.05 ± 0.1 cm), *Bromelia pinguin* (yellow round berry 2–3 cm, 5–15 seeds 0.3–0.4 cm diameter), *Bursera simaruba* (dehiscent trigonal capsule 0.1–0.15 cm, white-orange aril, single seed 0.7 ± 0.04 cm), *Capparis baduca* (brown-scarlet capsule 10×1 cm, 5 seeds), *Capparis indica* (brownish long-narrow dehiscent legume > 8 cm, red aril, 3–6 seeds 0.9 ± 0.3 cm), *Cayaponia attenuata* (green-orange round berry 1.1 cm, 1–2 seeds 0.8 ± 0.1 cm), *Diospyros nicaraguensis* (brown-orange round berry 1.9 cm, 1–2 seeds 1.1 ± 0.1 cm), *Casearia tremula* (red-orange capsule 2–3 cm, yellow inside, seed no data), *Samanea saman* (brown-redish flat legume 18.4 cm, 5–10 seeds 1.02 ± 0.1 cm), *Acacia collinsii* (brown flat legume 3.2 cm, yellow aril, 2–5 seeds 0.5 ± 0.1 cm), *Pithecellobium oblongum*

(red legume 14–16 cm, white aril, 4–6 seeds 0.8 ± 0.1 cm), *Trichilia martiana* (green capsule 1–1.5 cm, yellow aril, 2 seeds 1.15 ± 0.4 cm), *Hyperbaena tonduzii* (green subglobose drupe 1–1.5 cm, single seed 2.5 ± 0.1 cm), *Brosimum alicastrum* (greenish round drupe > 1.5 cm, single seed 1.5 ± 0.2 cm), *Maclura tinctoria* (greenish round berry > 1 cm, numerous seeds 0.3 ± 0.02 cm), *Ficus nitida* (greenish round syconium > 1 cm, numerous seeds 0.01 cm), *Ficus cotinifolia* (greenish round syconium, numerous seeds < 0.3 cm), *Ximena americana* (yellow round drupe 1.9 cm, single seed 1.5 ± 0.1 cm), *Passiflora platyloba* (yellow round-fleshy berry > 5 cm, numerous seeds 0.4 ± 0.03 cm), *Piper tuberculatum* (white berry infructescence, numerous seeds < 0.3 cm), *Coccoloba* sp. (pink round drupe 0.6 cm, single seed 0.5 ± 0.05 cm), *Guettarda macrosperma* (green-pink globose berry > 1.5 cm, 1–2 seeds 0.9 ± 0.3 cm), *Paullinia pinnata* (red long-narrow capsule 1.5–2 cm, white aril, single seed > 1 cm), *Allophylus occidentalis* (red globose drupe < 1 cm, single seed 0.6 ± 0.04 cm), *Muntingia calabura* (dark red round berry 1.1 cm, numerous seeds < 0.3 cm), *Phoradendron dipterum* (white-orange round drupe 0.5 cm, single seed), *Cissus alata* (black-dark purple round berry > 0.5 cm, numerous seeds).