Post-Dispersal Seed Removal and Germination Selected Tree Species Dispersed by Cebus capucinus on Barro Colorado Island, Panama

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ABSTRACT
Dispersal quality, an important component of seed disperser effectiveness, may strongly affect the rate of plant recruitment. Here we evaluated the quality of Cebus monkey dispersal by comparing the secondary removal fate and germination of fresh and Cebus-ingested seeds of nine tree species on Barro Colorado Island, Panama. Overall, rates of secondary seed removal by vertebrates were low, with most Cebus defecations remaining undisturbed for extended periods on the forest floor. Only four of 30 feces were completely buried by dung beetles, and we found significantly higher vertebrate removal of defecated seeds than control seeds for only one species, Cordia bicolor. Seed germination varied greatly between plant taxa. Seeds of 3 out of 9 species showed significantly higher percent germination after monkey gut passage than control fresh seeds. Germination times tended to be shorter for defecated than for control seeds but were significantly different only for one of nine species, Cecropia insignis. Low rates of seed removal from Cebus feces, coupled with high germination probabilities, suggest high dispersal effectiveness for Cebus and contrasts strongly with patterns of post-dispersal seed fate recorded for other primate species.

RESUMEN
La calidad de la dispersión, un componente importante de la efectividad de un dispersor de semillas, puede afectar marcadamente la tasa de reclutamiento de las plantas. Aquí nosotros evaluamos la calidad de dispersión de los monos Cebus, comparando el destino de la remoción secundaria y la germinación de semillas frescas y semillas ingeridas por Cebus para nueve especies de árboles en la Isla de Barro Colorado, Panamá. En general, las tasas de remoción secundaria de semillas por vertebrados fueron bajas, con la mayoría de las heces de Cebus permaneciendo sin perturbar por períodos prolongados sobre el suelo del bosque. Solo cuatro de 30 heces fueron completamente enterradas por escarabajos, y nosotros sólo encontramos significativamente mayor remoción por vertebrados en semillas defecadas que de semillas control para una especie, Cordia bicolor. La germinación de semillas varió ampliamente entre los diferentes taxa de plantas. Tres de nueve especies de semillas, mostraron un porcentaje de germinación significativamente mayor luego de pasar por el tracto digestivo de los monos que las semillas frescas de control. Los tiempos de germinación tendieron a ser más cortos para las semillas defecadas que para las semillas control, pero fueron significativamente diferentes sólo para una de nueve especies - Cecropia insignis. Bajas tasas de remoción de semillas de las heces de Cebus sumado a elevadas probabilidades de germinación, sugieren alta efectividad de dispersión por Cebus, y contrasta fuertemente con patrones de destino post-dispersión de semillas para otras especies de primates.

Key words: Barro Colorado Island; Cebus capucinus; dispersal effectiveness; dung beetle; germination; rodent; seasonal moist tropical forest; secondary seed dispersal; seed fate; seed removal.


Enhanced seed germination rates have been reported for seeds following vertebrate gut passage; however, effects are quite variable depending upon both the consumer and seeds consumed (Coughenour & Detling 1986, Lieberman & Lieberman 1986, Traveset & Verdú 2001). A critical dependence upon gut passage for germination is not expected given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002). Nonetheless, despite many reviews of the effects on seed dispersal given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen et al. 2002).

Primary dispersal by arboreal frugivores may also precede significant secondary seed removal and predation on the forest floor, resulting in plant spatial distributions that are distinct from initial dispersal patterns (Chambers & MacMahon 1994, Andresen 2001, Forget et al. 2001, Vander Wall 2001). In neotropical forests, seeds and fruits fallen from trees or dropped by flying and arboreal consumers may be removed and consumed by terrestrial animals (Dirzo & Domínguez 1986; Forget 1993, 2001; Zhang & Wang 1995; Sánchez-Cordero &

A variety of factors may influence whether seeds are encountered by predators and secondary dispersers on the ground. These include site conditions, such as litter coverage, influencing visual cues (Schupp 1988a,b; Willson 1988), seed density, proximity to fruiting trees influencing foraging patterns (Janzen 1970, 1971; Schupp 1988b; Forget & Milleron 1991; Forget 1993; Fragoso et al. 2003), and the presence of fecal material generating olfactory cues (Zhang & Wang 1995, Lambert et al. 2004). Thus, we might expect contrasting seed fates depending on both where seeds are deposited and how seeds are handled and consumed.

Here we examine the critical effects of seed consumption on the dispersal effectiveness of the white-faced monkey, Cebus capucinus (Linnaeus). Previous studies of this primate indicate its potential as an exceptionally effective seed disperser carrying seeds long distances, and depositing seeds in small clumps with relatively little fecal material (Wéhncke et al., 2003). Here we evaluate (1) the effect of the presence of Cebus feces on seed removal by invertebrates and vertebrates; (2) the effect of seed deposition microsite (beneath and 20 m away from fruiting trees) on the intensity of seed removal by invertebrates and vertebrates; and (3) the percentage and rate of seed germination for a sample of species defecated by Cebus.

METHODS

STUDY SITE.—The study was conducted in seasonally moist tropical forest in Barro Colorado Island (BCI), Panama (9°09′N, 79°51′W) (Croft 1978, Foster & Brokaw 1982). The climate in BCI is seasonal with a dry period from late December through mid April and a wet season having peak rainfall in October–November. Rainfall averages 2600 mm/yr and annual temperature averages 27°C. A description of the flora, fauna, and ecology can be found in Croft (1978) and Leigh (1999). The most abundant vertebrate seed predators and secondary dispersers on BCI are agoutis (Dasyprocta punctata, Gray 1842); red-tailed squirrels (Sciurus granatensis, Humboldt 1811); the spiny rat (Proechimys semispinosus, Tomes 1860); pacas (Cuniculus paca, Linnaeus 1776); and peccaries (Tayassu tajacu, Linnaeus 1758). The study was carried out early in the wet season (June 1999) when fruit availability is highest on BCI (Foster & Brokaw 1982).

Cebus effects on vertebrate seed removal.—To examine how Cebus monkeys influence post-dispersal seed removal rates we placed seeds with and without fecal material at two potential seed deposition sites: below and 20 m away from the crowns of fruiting Cordia bicolor A. DC., (Boraginaceae) trees. At each site we evaluated the fate of seeds of five species either imbedded in Cebus feces, or collected directly from fruits and set out without feces (controls). Control and fecal-embedded seeds were placed in plastic bowls 15 cm diameter, 4 cm tall buried flush with the soil surface. The number and species of seeds selected for this experiment were representative of seeds found in the feces of Cebus during the study period (Wéhncke et al. 2003). Treatment and control bowls were placed 1 m apart and each contained three seeds of C. bicolor, two seeds of Licania hypoleuca Benth. (Chrysobalanaceae), one seed of Lactuca panamensis (Woodson) Markgr. (Amaranthaceae), one seed of Rhedaelia edulis (Seem.) Planch & Triana (Guttiferae), and five seeds of Hasseltia floribunda Kunth (Flacourtiaeae). In total, paired treatment and control bowls were placed at ten below-crown sites and at 10 paired sites 20 m away.

C. bicolor was selected as the focal species in this study because its fruits are among the most frequently consumed by Cebus (see Appendix in Wéhncke et al. 2003), and because fruiting trees are abundant, widely distributed in the study area, and had large fruit crops during the study period. As we were unable to distinguish seed predation from secondary dispersal, we refer here to seed removal. In addition, we did not distinguish between seed removal by small and large rodents, and by other vertebrates. The steep sides of the plastic bowls used in this experiment prevented seeds from being removed by dung beetles. Transparent plastic shelters constructed 50 cm above the soil surface also protected seeds from litter coverage and from rain from washing away fecal material. The number of seeds removed from each bowl was recorded after 2, 5, 13, and 27 d of first placement. After the last census no more removal events were recorded. We used the Fisher exact test to test if the presence of feces and deposition site had any effect on seed removal.

Cebus effects on invertebrate seed removal.—We performed a second experiment to test whether Cebus gut passage and the proximity to fruiting trees had any effect on the rate of seed removal by dung beetles and ants. Seeds of three species were placed directly on the soil surface at sites directly beneath fruiting C. bicolor trees and 20 m from fruiting trees as before. Seeds used in this experiment were from Miconia argentea (Sw.) DC. Melastomataceae (0.5 mm length), Cecropia insignis Liebm. Cecropiaeae (1.25 mm length), and C. bicolor (8 mm length). Individual species were placed at separate locations >1 m apart and were either enclosed in Cebus feces or were removed directly from ripe, undispersed fruits. In total, one pair of fecal enclosed and fresh seed treatments for each species was placed below a different Cordia tree and non-Cordia site each day for 5 d.

To mimic the observed composition of Cebus defecations, each simulated fecal sample (average weight = 7.6 ± 3 g) contained 2500 M. argentea seeds, 1000 C. insignis seeds, or 1 C. bicolor seed. These numbers were obtained by dissecting fecal samples produced by Cebus monkeys and represent the modal number of seeds of these species in total fecal samples. Fresh seeds collected from ripe fruit were placed out in numbers characteristic of the mean clump size produced by passive dispersal of these species beneath the crowns of fruiting trees and consisted of 100 M. argentea seeds, 50 C. insignis seeds, and 3 C. bicolor seeds. Sets of seeds were observed for 6 h after the time they were set out. We registered the time of complete removal of feces and seeds, and also the time of arrival of each different beetle and ant species. Beetles were classified into two types according to the way feces were processed: “tunnelers” immediately buried seeds and feces at the site they were encountered whereas “rollers” removed seeds up to distances ranging between 6 and 250 cm (50.8 ± 55.1 cm, N = 18) before burial. Beetles were preserved
in 70 percent alcohol for later identification. At the end of the experiment, we determined how many seeds were left and the proportion of fecal material removed and buried. The mean number of *C. insignis* and *M. argentea* seeds removed from the two habitat types were compared using the paired samples *t* test.

**SEED GERMINATION.**—To examine whether seeds survive passage through the gut of *Cebus*, we removed seeds from fresh (<2-d old) *Cebus* feces and from fruits of the same species dropped to the ground to simulate natural conditions for germination. Seeds were washed before germination tests were performed on nine species (Table 1) representative of the wide range in size and morphology of seeds consumed by *Cebus* (see Appendix in Wehnicke et al. 2003). Small seeds (<0.5 cm) of six different species (*C. insignis*, *Cercopita obutusifolia* Bertol., *Ficus yoponensis* Desv., *H. floribunda*, *Miconia affinis* DC., and *M. argentea*) were placed on filter paper on Petri-dishes, and were kept in a growth chamber (12 h at 60 μmol/m²/s, red: far red 1.65, at 30 °C; 12 h dark at 25°C). Large seeds (>0.5 cm) of *C. bicolor*, *Cordia lasiocalyx* Pittier, and *R. edulis*) were placed in trays containing a mixture of sterilized soil and sand in a 3:1 proportion, and placed in a screened growing house (ca 20% full sun). Seeds were not washed before sowing in order to simulate natural conditions for germination. Seeds were watered when needed and emergent seedlings were counted and removed every 2–5 d. The number of seeds that germinated at the end of the experiment from fecal samples vs. dropped fruits was compared using the Mantel–Haenszel test, and the percentage and rate of seed germination were calculated. Germination trials ended three weeks after no further germination. Median germination times were compared using the Mann Whitney *U* test.

**RESULTS**

**VERTEBRATE SEED REMOVAL.**—After 27 d of observations, four of five species considered in this experiment experienced low levels of seed removal ranging from 8 percent for *C. bicolor* to 38 percent for *L. panamensis*. At the end of the study the numbers of seeds removed did not differ significantly between sites below and away from *Cordia* trees although more seeds tended to be removed from the below tree sites for three of the four species studied (Table 2). Presence of fecal material had a significant positive effect on removal only for *C. bicolor* seeds, with a marginal effect for *L. hypoleuca* (Table 2). Seeds of *H. floribunda* were excluded from this analysis because ants were observed entering the bowls and consuming the seeds. Furthermore, five seeds of *C. bicolor* and 29 seeds of *H. floribunda* germinated *in situ* during the 27-d period. Only 5 d were needed for 23 *H. floribunda* seeds to germinate.

**SEED REMOVAL BY DUNG BEETLES AND ANTS.**—Most (24/30) feces were visited by dung beetles or ants over the 5 d of the study. Two beetle species also visited seeds without fecal material but did not remove them. Dung beetles arrived at the feces on average after 65 ± 53 min (*N* = 24). Only four feces were buried completely, and therefore most of fecal enclosed seeds remained on the forest floor for an extended period. A total of 53 beetle species and 9 ants, 2 species, were observed at seed stations (Appendix). An average of 1.8 ± 1.3 (range 0–4) different beetles arrived at each fecal sample during the study (*N* = 30). During the first hours after the placement of feces on the floor, rollers were commonly attracted first. The mean number of beetles attracted to each fecal sample was the same in the two microsites (mean number of beetles for the two microsites = 1.7 ± 1.3, *N* = 15).

Beetles arrived at similar times to feces placed below and away from fruiting trees (mean time of beetle arrival: 68 ± 58 min, *N* = 11 and 62 ± 52 min, *N* = 13; respectively). All 11 of 30 feces rolled into balls by beetles contained seeds of *M. argentea* and *C. insignis*. In contrast, only two out of 30 *C. bicolor* seeds imbedded in feces were rolled away by dung beetles. Beetles moved dung balls at an average distance of 51 ± 55 cm (*N* = 18, range: 6–250 cm). Significantly more seeds of *M. argentea* (mean number of seed removed: 1220 ± 770, *N* = 15) and of *C. insignis* (mean number of seed removed: 490 ± 310, *N* = 15)

<p>| TABLE 1. | Total number of species of seeds defecated (treatment) and fresh (control) used in germination experiments. Total number of seeds and days of observation. Number of replicates is in parentheses. The first six species were germinated in a growth chamber. |</p>
<table>
<thead>
<tr>
<th>Species of seeds</th>
<th>Number of defecated seeds (trials)</th>
<th>Number of control seeds (trials)</th>
<th>Total seeds studied</th>
<th>Total days</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. insignis</em></td>
<td>350 (15)</td>
<td>350 (15)</td>
<td>700</td>
<td>59</td>
</tr>
<tr>
<td><em>C. obutusifolia</em></td>
<td>40 (2)</td>
<td>60 (2)</td>
<td>100</td>
<td>43</td>
</tr>
<tr>
<td><em>F. yoponensis</em></td>
<td>64 (3)</td>
<td>64 (3)</td>
<td>128</td>
<td>43</td>
</tr>
<tr>
<td><em>H. floribunda</em></td>
<td>27 (4)</td>
<td>90 (6)</td>
<td>117</td>
<td>47</td>
</tr>
<tr>
<td><em>M. affinis</em></td>
<td>100 (2)</td>
<td>100 (2)</td>
<td>200</td>
<td>29</td>
</tr>
<tr>
<td><em>M. argentea</em></td>
<td>1013 (22)</td>
<td>1016 (22)</td>
<td>2029</td>
<td>64</td>
</tr>
<tr>
<td><em>C. bicolor</em></td>
<td>95 (22)</td>
<td>28 (10)</td>
<td>123</td>
<td>12</td>
</tr>
<tr>
<td><em>C. lasiocalyx</em></td>
<td>53 (11)</td>
<td>53 (11)</td>
<td>106</td>
<td>24</td>
</tr>
<tr>
<td><em>R. edulis</em></td>
<td>14 (4)</td>
<td>10 (3)</td>
<td>24</td>
<td>12</td>
</tr>
</tbody>
</table>

<p>| TABLE 2. | Seed removal by vertebrates according to type of microhabitat and presence or absence of <em>Cebus</em> fecal material (see methods). |</p>
<table>
<thead>
<tr>
<th>Species of seeds</th>
<th>Seed removal from two types of microhabitats</th>
<th>Seed removal from feces and controls</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Percentage of seeds removed</td>
<td>Fisher exact test</td>
</tr>
<tr>
<td></td>
<td>Below (N)</td>
<td>Outside (N)</td>
</tr>
<tr>
<td><em>C. bicolor</em></td>
<td>12%</td>
<td>3%</td>
</tr>
<tr>
<td><em>L. hypoleuca</em></td>
<td>15%</td>
<td>10%</td>
</tr>
<tr>
<td><em>L. panamensis</em></td>
<td>33%</td>
<td>40%</td>
</tr>
<tr>
<td><em>R. edulis</em></td>
<td>17%</td>
<td>0%</td>
</tr>
</tbody>
</table>
imbedded in feces were removed by dung beetles from sites away from C. bicolor trees ($P < 0.05$ for both), than from sites below C. bicolor trees (mean number of seed removed: $917 \pm 885$, $N = 15$) and of C. insignis (mean number of seed removed: $367 \pm 354$, $N = 15$). Two ant species removed 30/500 seeds of M. argentea and 30/250 seeds of C. insignis lacking fecal material and from outside C. bicolor trees. We did not test differences in ant removal between locations because these data represent only two cases of seed removal by ants. Ants did not remove seeds from fecal material.

SEED GERMINATION.—Cebus ingestion altered seed germination success relative to uningested seeds for almost all species tested. Effects of Cebus ingestion, however, were not consistent among species. Of the nine species studied, four species had significantly higher germination of defecated than uningested seeds, and two species had significantly lower germination (Table 3). For the three remaining species there were either no significant differences in germination success or overall germination rates were too low to assess treatment effects. Gut passage had very little effect on the rate of seed germination. Seeds of C. insignis ingested by Cebus germinated significantly faster than control seeds ($U = 174$, $df = 1$, $P = 0.008$), but median time to germination was only a day earlier for defecated seeds. Median germination times for the remaining species varied from 6 (Hasseltia) to 77 d (Rheedia) and were not significantly different between treatments (Table 4).

**DISCUSSION**

Two factors that may alter patterns of primary seed dispersal in neotropical forests are the presence of fecal material around seeds (Janzen 1982a,b; Chapman 1989; Howe 1989; Zhang & Wang 1995) and the presence of high densities of fruits and seeds at sites where seeds are deposited (Janzen 1970, 1971; Sánchez-Cordero & Martínez-Gallardo 1998). Here, we show that for seeds dispersed by C. capucinus, neither the presence of feces, nor the seed deposition microsite had significant effects on post-dispersal seed removal by invertebrates and vertebrates. Furthermore, ingestion of seeds by Cebus failed to show strong and consistent effects on the success or rate of seed germination among the species evaluated.

These results contrast with previous studies showing that mammalian dung can attract dung beetles (Estrada & Coates-Estrada 1986, 1991; Estrada et al. 1993; Andresen 2001) and rodents (Janzen 1986, Andresen 1999). At least in the neotropics, some evidence suggests that it is the pattern in which seeds are defecated that is the crucial factor determining the rates of seed removal (Zhang & Wang 1995, Wehncke et al. 2004). Seeds are deposited by Cebus in a scattered manner along with relatively small amounts of fecal material, resulting in low seed removal rates (Zhang & Wang 1995, Wehncke et al. 2004). We predicted that seed survival in scattered, small fecal clumps should be higher, because a clumped pattern of defecation characteristic of most primate species constitutes a major visual or olfactory stimulus for seed predators. In this study, we found strikingly low seed removal rates from Cebus defecations, either by dung beetles, ants, or rodents. Other important dispersers of species consumed by Cebus on BCI (bats, tapiro, howler, and spider monkeys) are also capable of equally long-distance seed movement; however, they commonly deposit seeds in large clumps at feeding roosts, latrines, and/or sleep trees (Julliot 1996, Zhang & Wang 1995, Fragoso 1997, Thies 1998, Schupp et al. 2002, Fragoso et al. 2003, Wehncke et al. 2003). However, we should mention that Julliot (1997) working with howler monkeys and Rogers et al. (1998) with gorillas showed that seeds deposited in clumped patterns may also experience increased seedling survival.

On BCI, studies have generally reported high levels of secondary seed dispersal and predation by rodents (Forget & Milleron 1991; Forget 1992, 1993, 1996; Forget et al. 2001); however, these levels may vary depending on season and site. Seasonal variability in food availability coupled with spatial variation in food abundance probably strongly affects the fate of rodent removed seeds (Vander Wall 1990, Forget et al. 2001). For example, on BCI, agoutis, D. punctata, hoard considerably more seeds than they eat during the period of high fruit abundance (May–August) when this study was conducted (Smythe 1978, Forget et al. 2001). Thus, rodent population density and food availability may interact to create areas of low or high secondary seed dispersal or

### Table 3. Percentage of germination for defecated vs. control species of seeds. Numbers of replicates detailed in Table 1. *Represent cases in which germination percentages were higher for defecated than for control seeds.

<table>
<thead>
<tr>
<th>Seed species</th>
<th>Defecated seeds (%)</th>
<th>Control seeds (%)</th>
<th>Mantel-Haenszel chi-square $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. insignis</td>
<td>83% (350)</td>
<td>100% (350)</td>
<td>43.199 &lt;0.01</td>
</tr>
<tr>
<td>C. obtusifolia</td>
<td>67% (40)</td>
<td>10% (60)</td>
<td>42.948 &lt;0.01*</td>
</tr>
<tr>
<td>F. yponennis</td>
<td>85% (64)</td>
<td>0 (64)</td>
<td>—</td>
</tr>
<tr>
<td>H. floribunda</td>
<td>84% (27)</td>
<td>77% (90)</td>
<td>4.950 &lt;0.05*</td>
</tr>
<tr>
<td>M. affinis</td>
<td>96% (100)</td>
<td>82% (100)</td>
<td>8.995 &lt;0.01*</td>
</tr>
<tr>
<td>M. argentea</td>
<td>64% (1013)</td>
<td>99% (1016)</td>
<td>457.694 &lt;0.01</td>
</tr>
<tr>
<td>C. bicolor</td>
<td>18% (95)</td>
<td>0 (28)</td>
<td>—</td>
</tr>
<tr>
<td>C. lasiocalyx</td>
<td>20% (53)</td>
<td>41% (53)</td>
<td>0.816 &gt;0.05</td>
</tr>
<tr>
<td>R. edulis</td>
<td>68% (14)</td>
<td>71% (10)</td>
<td>2.438 &gt;0.05</td>
</tr>
</tbody>
</table>

### Table 4. Mean time at which the 50% of defecated and control seeds germinated.

<table>
<thead>
<tr>
<th>Species</th>
<th>Defecated seeds</th>
<th>Control seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean T50 (d)</td>
<td>Rank sum</td>
<td>Mean T50 (d)</td>
</tr>
<tr>
<td>C. insignis</td>
<td>7</td>
<td>171</td>
</tr>
<tr>
<td>C. obtusifolia</td>
<td>10.5</td>
<td>4</td>
</tr>
<tr>
<td>F. yponennis</td>
<td>11</td>
<td>9</td>
</tr>
<tr>
<td>H. floribunda</td>
<td>6.5</td>
<td>16</td>
</tr>
<tr>
<td>M. affinis</td>
<td>11</td>
<td>4</td>
</tr>
<tr>
<td>M. argentea</td>
<td>15.3</td>
<td>451.5</td>
</tr>
<tr>
<td>C. bicolor</td>
<td>35.5</td>
<td>343</td>
</tr>
<tr>
<td>C. lasiocalyx</td>
<td>31.5</td>
<td>134</td>
</tr>
<tr>
<td>R. edulis</td>
<td>70.5</td>
<td>14.5</td>
</tr>
</tbody>
</table>
predation (Notman et al. 1996; Forget et al. 2000, 2001). Low removal rates reported here may not necessarily translate to significantly higher recruitment rates for Cebus dispersed seeds. Here, we referred only to short-term seed survival after deposition, whereas the best site for seed survival may not necessarily be the best site for sapling recruitment. Further studies on seed fate are needed to confirm this.

Although some studies report density-dependent seed removal for several plant species in the neotropics (Howard et al. 1985, Schupp 1988a, Sánchez-Cordero & Martínez-Gallardo 1998), our results agree with those that reported an absence of distance effects (Molofsky & Fisher 1993, Terborgh et al. 1993) or levels of predation independent of habitat (Forget & Milleron 1991). Lambert (1997, 2001) in the paleotropics found similar independence of predation with microhabitat and treatment, but, by contrast, showed severe levels of post-dispersal seed predation. Because our study focused on a selected set of seed species swallowed and dispersed by Cebus, and a single tree species was used to evaluate microsite effects, we should be cautious in making general conclusions. However, these species were selected because they well-represented species dispersed by Cebus at the study period and those species able to be removed by potential predators of small to medium-sized seeds (up to ca 1.5-cm long). In summary, low rates of seed removal in fruit and seed-rich areas may depend on food availability elsewhere in the forest and on the quality of food resources available (Brewer 2001, Forget et al. 2001). Therefore, we could suggest that high availability and/or better quality of food resources in other parts of the forest might explain overall low rates of seed removal in this experiment during the study period.

In this study, similar mean numbers of dung beetles were attracted to locations below fruiting C. bicolor trees and to locations with no fruiting trees. The time of first arrival of dung beetles was also similar in both sites. Seed burial by dung beetles is considered to have a strong influence on seed survival by preventing seed predation and desiccation (Andersen 1999, 2002). However, the depth at which beetles bury seeds can also reduce germination success (Dalling et al. 1994, Shepherd & Chapman 1998, Feer 1999). In this study, most of the seeds remained imbedded in feces on the forest floor and experienced low removal rates. In the case of the largest seeded species, C. bicolor, only 2 out of 30 seeds were buried by dung beetles. As a consequence, species that are most likely to benefit from escape from rodent predation through burial and are most likely to successfully emerge from beneath several centimeters of soil may be least likely to be incorporated into beetle dung balls.

Earlier work has indicated that C. capucinus is a very effective (e.g., sensu Schupp 1993, 2002) seed dispersal agent (Zhang & Wang 1995, Wehncke et al. 2003). On BCI it has been shown that Cebus manipulate and consume a remarkably high diversity of fruit species, from which seeds of the majority are found intact in feces in a viable state (Wehncke et al. 2003). Combinations of characteristics such as short feeding bouts, asynchronous small defecations of individuals within the group, and short gut retention times contribute to the seed defecation pattern produced by Cebus. As a consequence of these characteristics, most of the seeds receive a gentle treatment by Cebus, they are dispersed to long distances, and are deposited in a widely spaced spatial pattern. These are among the clearest advantages accruing to those ingested seeds because they have the opportunity to escape from the increased risk of mortality around the neighborhood of the parent plant, and to colonize new and potentially more favorable microsites for seedling establishment (Howard & Smallwood 1982).

According to Howe’s (1989) “scatter- and clump-dispersal” hypothesis, “scatter-dispersed” plant species are unlikely to evolve tolerance against density-dependent factors (chemical and/or mechanical defenses against competitors, seed predators, and pathogens) because they recruit to the seedling stage as isolated individuals. Here, we found a high variation of the effect of Cebus ingestion on germination success among seed species, and almost no effect on the rate of germination. We suggest that although seed deposition patterns have important implications for short-term seed survival (Wehncke et al. 2004) at least in a neotropical dry forest, variations in seed ingestion and handling between and within dispersers and habitats may contribute to attenuate any possible adaptation of plants to differences between scatter- and clump-dispersal strategies.

Finally, as the dispersal quality provided by any given animal is not constant (Wehncke et al. 2004) and may depend on the particular ecological scenario where dispersal takes place, the relationship among a series of factors (environmental and those occurring between animal frugivory, seed deposition, and seed fate) influence the ultimate fate of the seed dispersed. Although here we provide data regarding the possible role of post-dispersal agents and effect of gut passage on seed germination, more comparative work is still needed to evaluate the relative contributions of members of diverse disperser communities to plant recruitment success in contrasting habitats.

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LITERATURE CITED


Appendix. Species of dung beetles attracted to C. capucinus feces. Number of individuals captured during the experiment in each ecological category: tunneler = 32, roller = 26.

<table>
<thead>
<tr>
<th>Hybosoridae</th>
<th>Scarabaeidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anaides fossulatus Westwood 1846, Venezuela</td>
<td>Atreuchus candezai (Harold)</td>
</tr>
<tr>
<td>Coelodes castaneus Westwood 1846, Colombia, Costa Rica, Nicaragua</td>
<td>Atreuchus howdeni Kohlmann</td>
</tr>
<tr>
<td></td>
<td>Ateuchus candezei (Harold) Tunneler</td>
</tr>
<tr>
<td></td>
<td>Ateuchus howdeni Kohlmann Tunneler</td>
</tr>
<tr>
<td></td>
<td>Cathidium ardens Bates Tunneler</td>
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<tr>
<td></td>
<td>Canthidium elegantulum Balthasar Tunneler</td>
</tr>
<tr>
<td></td>
<td>Canthidium haroldi Preudhomme Tunneler</td>
</tr>
<tr>
<td></td>
<td>Canthidium tuberifrom Howden &amp; Young Tunneler</td>
</tr>
<tr>
<td></td>
<td>Canthion aequinoctialis Harold Roller</td>
</tr>
<tr>
<td></td>
<td>Canthion angustatus Harold Roller</td>
</tr>
<tr>
<td></td>
<td>Canthion cyanellus sallei Harold Roller</td>
</tr>
<tr>
<td></td>
<td>Canthion eurycetes Bates Roller</td>
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<tr>
<td></td>
<td>Canthion monilatus Bates Roller</td>
</tr>
<tr>
<td></td>
<td>Canthion septemmaculatus (Latreille) Roller</td>
</tr>
<tr>
<td></td>
<td>Canthion subhyalinus Harold Roller</td>
</tr>
<tr>
<td></td>
<td>Onthophagus dicrocinus Bates Tunneler</td>
</tr>
<tr>
<td></td>
<td>Onthophagus sharpi Harold Tunneler</td>
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</tbody>
</table>