

Post-Dispersal Seed Removal and Germination Selected Tree Species Dispersed by *Cebus capucinus* on Barro Colorado Island, Panama¹

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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 mas 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.

IN SPECIES-RICH PLANT COMMUNITIES EFFECTIVE DISPERSAL OF SEEDS is critical to seedling recruitment (Dirzo & Domínguez 1986, Zhang & Wang 1995, Wenny 2000, Bleher & Böhning-Gaese 2001, Schupp *et al.* 2001). The spatial pattern in which seeds are deposited and the treatment that seeds receive characterize the quality of seed dispersal (Schupp 1993, 2002; Zhang & Wang 1995; Fragoso *et al.* 2003; Wehncke *et al.* 2004). Important potential treatment effects of dispersers include influencing seed viability through mastication and passage through the digestive tract (Traveset & Verdú 2001) and influencing post-dispersal fate by altering the probability that seeds encounter predators and secondary dispersers (Chapman 1989, Zhang & Wang 1995, Lambert 2001, Andresen 2002, Laborde & Thompson 2004, Wehncke *et al.* 2004).

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 by vertebrates (Howe & Smallwood 1982, Leighton & Leighton 1983, Gautier-Hion *et al.* 1985, Levey *et al.* 2001), we still do not know the consistency with which animals affect the germination of different plant species.

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 &

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Martínez-Gallardo 1998; Andresen 1999). These include invertebrates like dung beetles and ants (Andresen 1999, 2002; Levey & Byrne 1993, Terborgh *et al.* 1993) and vertebrates like peccaries and rodents (Morris 1962, Smythe 1978, Sánchez-Cordero & Martínez-Gallardo 1998, Forget *et al.* 2001, Theimer 2001, García *et al.* 2004). Post-dispersal seed removal at small spatial scales by dung beetles and ants may further influence the probability of seedling establishment by preventing seed desiccation and predation (Price & Jenkins 1986, Andresen 1999, Gammans *et al.* 2004).

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 2001, Wehncke *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 (Wehncke *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) (Croat 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 Croat (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 (*Coniculus 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 (Wehncke *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 *Lacmellea panamensis* (Woodson) Markgr. (Apocynaceae), one seed of *Rheedia edulis* (Seem.) Planch & Triana (Guttiferae), and five seeds of *Hasseltia floribunda* Kunth (Flacourtiaceae). 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 Wehncke *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. Cecropiaceae (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

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.

Species of seeds	Number of defecated seeds (trials)	Number of control seeds (trials)	Total seeds studied	Total days
<i>C. insignis</i>	350 (15)	350 (15)	700	59
<i>C. obtusifolia</i>	40 (2)	60 (2)	100	43
<i>F. yoponensis</i>	64 (3)	64 (3)	128	43
<i>H. floribunda</i>	27 (4)	90 (6)	117	47
<i>M. affinis</i>	100 (2)	100 (2)	200	29
<i>M. argentea</i>	1013 (22)	1016 (22)	2029	64
<i>C. bicolor</i>	95 (22)	28 (10)	123	12
<i>C. lasiocalyx</i>	53 (11)	53 (11)	106	24
<i>R. edulis</i>	14 (4)	10 (3)	24	12

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 during primate feeding bouts. 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 Wehcnke *et al.* 2003). Small seeds (<0.5 cm) of six different species (*C. insignis*, *Cecropia obtusifolia* 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 $\mu\text{mol}/\text{m}^2/\text{s}$, 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

TABLE 2. Seed removal by vertebrates according to type of microhabitat and presence or absence of *Cebus* fecal material (see methods).

Species of seeds	Seed removal from two types of microhabitats			Seed removal from feces and controls		
	Percentage of seeds removed		Fisher exact test (<i>P</i>)	Percentage of seeds removed		Fisher exact test (<i>P</i>)
	Below (<i>N</i>)	Outside (<i>N</i>)		Feces (<i>N</i>)	No feces (<i>N</i>)	
<i>C. bicolor</i>	12% (60)	3% (60)	0.163	13% (60)	2% (60)	0.032
<i>L. hypoleuca</i>	15% (40)	10% (40)	0.737	20% (40)	5% (40)	0.087
<i>L. panamensis</i>	33% (8)	40% (8)	1.00	62% (8)	12% (8)	0.119
<i>R. edulis</i>	17% (5)	0% (5)	1.00	20% (5)	0% (5)	1.00

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 , $N = 15$)

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.

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

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 ± 885 , $N = 15$) and of *C. insignis* (mean number of seed removed: 367 ± 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,

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

Species	Defecated seeds		Control seeds	
	Mean T50 (d)	Rank sum	Mean T50 (d)	Rank sum
<i>C. insignis</i>	7	171	8.5	294
<i>C. obtusifolia</i>	10.5	4	14	6
<i>F. yoponensis</i>	11	9	12	12
<i>H. floribunda</i>	6.5	16	5.5	39
<i>M. affinis</i>	11	4	14	6
<i>M. argentea</i>	15.3	451.5	16.3	538.5
<i>C. bicolor</i>	35.5	343	38	185
<i>C. lasiocalyx</i>	31.5	134	30	119
<i>R. edulis</i>	70.5	14.5	77	13.5

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, tapirs, 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

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 (Howe *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 (Andresen 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 (Howe & 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

- ANDRESEN, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a peruvian rain forest. *Biotropica* 31: 145–158.
- . 2001. Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *J. Trop. Ecol.* 17: 61–78.
- . 2002. Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica* 34: 261–272.
- ASQUITH, N. M., S. J. WRIGHT, AND M. J. CLAUSS. 1999. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* 78: 941–946.
- BLEHER, B., AND K. BÖHNING-GAESE. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129: 385–394.

- BREWER, S. W. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92: 245–255.
- BREWER, S. W., AND M. REJMANEK. 1999. Small rodents as significant dispersers of tree seeds in a neotropical forest. *J. Vegetat. Sci.* 10: 165–174.
- CHAMBERS, J. C., AND J. A. MACMAHON. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. *Ann. Rev. Ecol. System.* 25: 263–292.
- CHAPMAN, C. A. 1989. Primate seed dispersal: The fate of dispersed seeds. *Biotropica* 21: 148–154.
- . 1995. Primate seed dispersal: Coevolution and conservation implications. *Evolut. Anthropol.* 4: 73–110.
- , AND L. J. CHAPMAN. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *J. Trop. Ecol.* 12: 491–504.
- CLARK, D. A., AND D. B. CLARK. 1984. Spacing dynamic of a tropical rain forest tree: Evaluation of the Janzen–Connell model. *Am. Nat.* 124: 769–788.
- COUGHENOUR, M. B., AND J. K. DETLING. 1986. *Acacia tortilis* seed germination responses to water potential and nutrients. *Afr. J. Ecol.* 24: 203–205.
- CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California.
- DALLING, J. W. 2002. Ecología de semillas. In M. R. Guariguata and G. H. Kattan (Eds.). *Ecología y Conservación de Bosques Neotropicales*, pp. 345–375. Libro Universitario Regional, Costa Rica.
- , M. D. SWAINE, AND N. C. GARWOOD. 1994. Effect of soil depth on seedling emergence in tropical soil seed-bank investigations. *Funct. Ecol.* 9: 119–121.
- DE STEVEN, D., AND F. E. PUTZ. 1984. Impact of mammals on early recruitment of the tropical canopy tree *Dipteryx panamensis* in Panama. *Oikos* 43: 207–216.
- DIRZO, R., AND C. A. DOMÍNGUEZ. 1986. Seed shadows, seed predation and the advantages of dispersal. In A. Estrada and T. H. Fleming (Eds.). *Frugivores and seed dispersal*, pp. 237–249. Dr. W. Junk Publishers, Dordrecht.
- EMMONS, L. H., AND F. FEER. 1990. *Neotropical rainforest mammals. A field guide*. University of Chicago Press, Chicago, USA.
- ESTRADA, A., AND R. COATES-ESTRADA. 1986. Frugivory in howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: Dispersal and fate of seeds. In A. Estrada and T. H. Fleming (Eds.). *Frugivores and seed dispersers*, pp. 94–104. Dr. W. Junk Publishers, Dordrecht.
- . 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: Ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 9: 45–54.
- , G. HALFFTER, R. COATES-ESTRADA, AND D. A. MERITT. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 9: 45–54.
- FEER, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. *J. Trop. Ecol.* 15: 129–142.
- FENNER, M. 1987. Seedlings. *New Phytologist* 106(Supplement): 35–47.
- FORGET, P. M. 1990. Seed dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *J. Trop. Ecol.* 6: 459–468.
- . 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24: 408–414.
- . 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94: 255–261.
- . 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *J. Trop. Ecol.* 12: 751–761.
- , AND T. MILLERON. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87: 596–599.
- , E. MUÑOZ, AND E. F. LEIGH. 1994. Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panamá. *Biotropica* 26: 420–426.
- , T. MILLERON, F. FEER, O. HENRY, AND G. DUBOST. 2000. Effects of dispersal pattern and mammalian herbivores on seedling recruitment for *Virola michelii* (Myristicaceae) in French Guiana. *Biotropica* 32: 452–462.
- , D. S. HAMMOND, T. MILLERON, AND R. THOMAS. 2001. Seasonality of fruiting and fruit hoarding by rodents in neotropical forests: Consequences for seed dispersal and seedling recruitment. In D. J. Levey, W. R. Silva and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 241–256. CABI Publishing, UK.
- FOSTER, R. B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. In A. Rand and E. Leigh (Eds.). *The ecology of a tropical forest*, pp. 151–172. Smithsonian Institution Press, Washington, D.C.
- , AND N. V. L. BROKAW. 1982. Structure and history of the vegetation of Barro Colorado Island. In A. Rand and E. Leigh (Eds.). *The ecology of a tropical forest*, pp. 67–81. Smithsonian Institution Press, Washington, D.C.
- FRAGOSO, J. M. 1997. Tapir-generated seed shadows: Scale-dependent patchiness in the Amazon rain forest. *J. Ecol.* 85: 519–529.
- , K. M. SILVIUS, AND J. A. CORREA. 2003. Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* 84: 1998–2006.
- GAMMANS, N., K. SCHONROGGE, J. BULLOCK, AND M. FENNER. 2004. Reduction of seed predation by ant dispersal. In Book of abstracts, p. 99, seed ecology 2004, International Meeting on Seeds and the Environment, Rhodes, Greece.
- GARCÍA, D., J. R. OBESO, AND I. MARTÍNEZ. 2004. Post-dispersal seed predation modulates recruitment potential among bird-dispersed trees in Cantabrian forest. In Book of abstracts, p. 100, seed ecology 2004, International Meeting on Seeds and the Environment, Rhodes, Greece.
- GAUTIER-HION, A., J.-M. DUPLANTIER, R. QURIS, F. FEER, C. SOURD, J.-P. DECOUX, G. DUBOST, L. EMMONS, C. ERARD, P. HECKETSWEILER, A. MOUNGAZI, C. ROUSSILLON, AND J.-M. THIOLLAY. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324–337.
- GIACALONE-MADDEN, J., W. E. GLANZ, AND E. G. LEIGH. 1990. Adición: Fluctuaciones poblacionales a largo plazo de *Sciurus granatensis* en relación con la disponibilidad de frutos. In E. G. Leigh, A. S. Rand and D. M. Windsor (Eds.). *Ecología de un bosque tropical*, pp. 331–336. Smithsonian Tropical Research Institute, Balboa, Panama.
- GLANZ, W. E. 1990. Mammalian densities at protected versus hunted sites in Central Panama. In J. G. Robinson and K. H. Redford (Eds.). *Neotropical wildlife use and conservation*, pp. 163–173. The University of Chicago Press, Chicago, Illinois.
- , R. W. THORINGTON, J. GIACALONE-MADDEN, AND L. R. HEANEY. 1982. Seasonal food use and demographic trends in *Sciurus granatensis*. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: Seasonal rhythms and long-term changes*, pp. 239–252. Smithsonian Institution Press, Washington D.C.
- HALLWACHS, W. 1986. Agoutis *Dasyprocta punctata*: The inheritors of guapinol *Hymenaea courbaril* (Leguminosae). In A. Estrada and T. H. Fleming (Eds.). *Frugivores and seed dispersal*, pp. 119–135. Dr. W. Junk Publishers, The Hague.
- HARMS, K. E., S. J. WRIGHT, O. CALDERON, A. HERNANDEZ, AND E. A. HERRE. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493–495.

- HOWE, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. In R. David (Ed.). Seed dispersal, pp. 123–189. Academic Press, London, UK.
- . 1989. Scatter- and clump-dispersal and seedling demography: Hypothesis and implications. *Oecologia* 79: 417–426.
- , AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. System.* 13: 201–228.
- , E. SCHUPP, AND L. C. WESTLEY. 1985. Early consequences of seed dispersal for a neotropical tree. *Ecology* 66: 781–791.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- . 1971. Seed predation by animals. *Ann. Rev. Ecol. System.* 2: 465–492.
- . 1982a. Removal of seeds from horse dung by tropical rodents: Influence of habitat and amount of dung. *Ecology* 63: 1887–1900.
- . 1982b. Attraction of *Liomys* mice to horse dung and the extinction of this response. *Anim. Behav.* 30: 483–489.
- . 1986. Mice, big mammals, and seeds: It matters who defecates what where. In A. Estrada and T. H. Fleming (Eds.). *Frugivores and seed dispersal*, pp. 93–104. Dr. W. Junk Publishers, The Hague.
- JULLIOT, C. 1996. Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *Int. J. Primatol.* 17: 239–258.
- . 1997. Impact of seed dispersal by red howler monkeys (*Alouatta seniculus*) on the seedling population in the understory of tropical rain forests. *J. Ecol.* 85: 431–440.
- LABORDE, F. J., AND K. THOMPSON. 2004. Post-dispersal seed removal of hazel (*Corylus avellana* L.) in grassland. In *Book of Abstracts, p. 134, Seed Ecology 2004*, International Meeting on Seeds and the Environment, Rhodes, Greece.
- LAMBERT, J. E. 1997. Digestive strategies, fruit processing, and seed dispersal in the chimpanzees (*Pan troglodytes*) and redtail monkeys (*Cercopithecus ascanius*) of Kibale National Park, Uganda. Ph.D. Thesis, University of Illinois, Urbana-Champaign.
- . 2001. Exploring the link between animal frugivory and plant strategies: The case of primate fruit processing and post-dispersal seed fate. In D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 365–379. CABI Publishing, UK.
- LEIGH, E. G. 1990. Introducción. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). *Ecología de un Bosque Tropical: Ciclos estacionales y cambios a largo plazo*, pp. 15–23. Smithsonian Tropical Research Institute, Balboa, Panama.
- . 1999. Tropical forest ecology. A view from Barro Colorado Island. Oxford University Press, New York.
- , S. J. JR., WRIGHT, F. E. PUTZ, AND E. A. HERRE. 1993. The decline of tree diversity on newly isolated tropical islands: A test of a null hypothesis and some implications. *Evolut. Ecol.* 7: 76–102.
- LEIGHTON, M., AND D. R. LEIGHTON. 1983. Vertebrate response to fruiting seasonality within a Bornean rain forest. In S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). *Tropical rain forest ecology and management*, pp. 181–196. Blackwell Science, London, UK.
- LEVEY, D. J., AND M. M. BYRNE. 1993. Complex ant-plant interactions: Rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74: 1802–1812.
- , W. R. SILVA, AND M. GALETTI. 2001. Seed dispersal and frugivory: Ecology, evolution and conservation, p. 511. CABI Publishing, UK.
- LIEBERMAN, M., AND D. LIEBERMAN. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *J. Trop. Ecol.* 2: 113–126.
- MARTÍNEZ-GALLARDO, R., AND V. SÁNCHEZ-CORDERO. 1993. Dietary value of fruits and seeds to spiny pocket mice (Heteromyidae). *J. Mammal.* 74: 436–442.
- MILLER, M. F. 1994. Large African herbivores, bruchid beetles and their interactions with Acacia seeds. *Oecologia* 97: 265–270.
- MITCHELL, B. J. 1989. Resources, group behavior, and infant development in white-faced capuchin monkeys, *Cebus capucinus*. Ph.D. thesis, University of California, Berkeley.
- MOLOFSKY, J., AND B. L. FISHER. 1993. The effect of habitat and predation on seedling survival and growth of three shade-tolerant tree species in Panama. *Ecology* 74: 261–265.
- MORRIS, D. 1962. The behavior of the green acouchi (*Myoprocta pratti*) with special reference to scatter hoarding. *Zool. Soc. London Proc.* 139: 701–733.
- MORRISON, D. W. 1980. Foraging and day-roosting dynamics of canopy fruit bats in Panama. *J. Mammal.* 61: 20–29.
- NATHAN, R., AND H. C. MULLER-LANDAU. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15: 278–285.
- NOTMAN, E., D. L. GORCHOV, AND F. CORNEJO. 1996. Effect of distance, aggregation, and habitat on levels of seed predation for two mammal-dispersed neotropical rain forest tree species. *Oecologia* 106: 221–227.
- OVERDORFF, D. J., AND S. G. STRAIT. 1998. Seed handling by three prosimian primates in southeastern Madagascar: Implications for seed dispersal. *Am. J. Primatol.* 45: 69–82.
- POULSEN, R. J., C. J. CLARK, E. F. CONNOR, AND T. B. SMITH. 2002. Differential resource use by primates and hornbills: Implications for seed dispersal. *Ecology* 83(1): 228–240.
- PRICE, M. V., AND S. H. JENKINS. 1986. Rodents as seed consumers and dispersers. In D. R. Murray (Ed.). *Seed dispersal*, pp. 191–235. Academic Press, Sydney, Australia.
- ROGERS, M. E., B. C. VOYSEY, K. E. MCDONALD, R. J. PARNELL, AND C. E. G. TUTIN. 1998. Lowland gorillas and seed dispersal: The importance of nest sites. *Am. J. Primatol.* 45: 45–68.
- ROWELL, T. E., AND B. J. MITCHELL. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *J. Trop. Ecol.* 7: 269–274.
- SÁNCHEZ-CORDERO, V., AND R. MARTÍNEZ-GALLARDO. 1998. Postdispersal fruit and seed removal by forest-dwelling rodents in a lowland rainforest in México. *J. Trop. Ecol.* 14: 139–151.
- SCHUPP, E. W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76: 525–530.
- . 1988b. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51: 71–78.
- . 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. In A. Estrada and T. H. Fleming (Eds.). *Frugivores and seed dispersal*, pp. 15–29. Dr. W. Junk Publishers, Dordrecht.
- . 2002. The efficacy of the dispersal agent. In M. R. Guariguata and G. H. Kattan (Eds.). *Ecología y Conservación de Bosques Neotropicales*, pp. 357–360. Libro Universitario Regional, Costa Rica.
- , MILLERON, T., AND S. E. RUSSO. 2001. Dissemination limitation and the origin and maintenance of species-rich tropical forests. In D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 19–33. CABI Publishing, UK.
- SHEPHERD, V. E., AND C. A. CHAPMAN. 1998. Dung beetles as secondary seed dispersers: Impact of seed predation and germination. *J. Trop. Ecol.* 14: 199–215.
- SMYTHE, N. 1970. Relationship between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* 104: 25–35.

- . 1978. The natural history of the Central American agouti (*Dasyprocta punctata*). *Smithsonian Contrib. Zoology* 257: 1–52.
- . 1986. Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. *Ann. Rev. Ecol. System.* 17: 169–188.
- , W. E. GLANZ, AND E. G. LEIGH. 1982. Population regulation in some terrestrial frugivores. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: Seasonal rhythms and long-term changes*, pp. 227–238. Smithsonian Institution Press, Washington D.C.
- SORK, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68: 1341–1350.
- TERBORGH, J., E. LOSOS, M. P. RILEY, AND M. BOLAÑOS RILEY 1993. Predation by vertebrates and invertebrates on seeds of five canopy tree species of an Amazonian forest. *Vegetatio* 107/108: 375–386.
- THEIMER, T. C. 2001. Seed scatter-hoarding by white-tailed rats: Consequences for seedling recruitment by an Australian rain forest tree. *J. Trop. Ecol.* 17: 177–189.
- THIES, W. 1998. Resource and habitat use in two frugivorous bat species (Phyllostomidae: *Carollia perspicillata* and *C. castanea*) in Panama: Mechanisms of coexistence. Ph.D. thesis, University of Tübingen, Germany.
- TRAVESSET, A., AND M. VERDÚ. 2001. A meta-analysis of the effect of gut treatment on seed germination. In D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 339–350. CABI Publishing, UK.
- VANDER WALL, S. B. 1990. *Food hoarding in animals*. University of Chicago Press, Chicago.
- . 1994. Removal of wind-dispersed pine seeds by ground-foraging vertebrates. *Oikos* 69: 125–132.
- . 2001. Secondary dispersal of jeffrey pine seeds by rodent scatter-hoarders: The roles of pilfering, recaching and a variable environment. In D. J. Levey, W. R. Silva, and M. Galetti (Eds.). *Seed dispersal and frugivory: Ecology, evolution and conservation*, pp. 193–208. CABI Publishing, UK.
- WEHNCKE, E. V., S. P. HUBBELL, R. B. FOSTER, AND J. W. DALLING. 2003. Seed dispersal patterns produced by white-faced monkeys: Implications for the dispersal limitation of neotropical tree species. *J. Ecol.* 91: 677–685.
- , C. N. VALDEZ, AND C. A. DOMÍNGUEZ. 2004. Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: Consequences for seed dispersal effectiveness. *J. Trop. Ecol.* 20: 535–544.
- WENNY, D. G. 2000. Seed dispersal, seed predation and seedling recruitment of a neotropical tree. *Ecol. Monographs* 70: 331–351.
- WHELAN, C. J., M. F. WILSON, C. A. TUAM, AND I. SOUZA-PINTO 1991. Spatial and temporal patterns of post-dispersal seed predation. *Can. J. Botany* 69: 428–436.
- WILLSON, M. F. 1988. Spatial heterogeneity of post-dispersal survivorship of Queensland rainforest seeds. *Aust. J. Ecol.* 13: 137–146.
- WRIGHT, S. J., C. CARRASCO, O. CALDERON, AND S. PATON. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80: 1632–1647.
- ZHANG, S. Y., AND L. X. WANG. 1995. Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica* 27: 397–401.

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

Hybosoridae

Anaides fossulatus Westwood 1846, Venezuela

Coilodes castaneus Westwood 1846, Colombia, Costa Rica, Nicaragua

Scarabaeidae

Ateuchus candezei (Harold)

Ateuchus howdeni Kohlmann

Cathidium ardens Bates

Canthidium elegantulum Balthasar

Canthidium haroldi Preudhomme

Canthidium tuberifrons Howden & Young

Canthon aequinoctialis Harold

Canthon angustatus Harold

Canthon cyanellus sallei Harold

Canthon euryscelis Bates

Canthon moniliatus Bates

Canthon septemmaculatus (Latreille)

Canthon subhyalinus Harold

Onthophagus dicranius Bates

Onthophagus sharpi Harold

Scarabaeinae

Tunneler

Tunneler

Tunneler

Tunneler

Tunneler

Tunneler

Roller

Roller

Roller

Roller

Roller

Roller

Roller

Tunneler

Tunneler