

Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest

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ABSTRACT. The dispersal of seeds by howler monkeys (*Alouatta seniculus*) and the role of dung beetles in determining the fate of the dispersed seeds were studied at Nouragues Station, French Guiana, during three 2-mo periods (April–May, 1995–97). Howler monkeys were observed to disperse seeds of 47 plant species. Monkey dung attracted 57 species of dung beetles (Scarabaeidae), including tunnellers (maximum size 37 mm) and ball rollers (12.6 mm). The rate of seed burial was negatively correlated with seed size (10 plant species) and positively correlated with dung beetle size (six species of tunnellers). More than 80% of small seeds (< 5 mm) and 30% of large seeds (22 mm), were buried by the largest tunnellers. Dung beetles buried 13 to 23% of seeds ranging 8–13 mm in width. The maximum average depth of burial was 28 cm and varied according to the species of dung beetle. The rate of disappearance of large dung clumps varied during the day and was completed by nocturnal dung beetles. Seeds of *Chrysophyllum lucentifolium* (Sapotaceae) buried at 5 and 10 cm depths did not suffer predation, but showed low germination success compared to seeds left at the soil surface. Dung beetles affected the survival and distribution of a portion of the seeds dispersed by monkeys, and their relative importance in shaping seed fate depended on seed and beetle size.

KEY WORDS: *Alouatta seniculus*, dung beetles, French Guiana, rain forest, Scarabaeidae, seed dispersal

INTRODUCTION

Primates of neotropical forests are largely frugivorous and important seed dispersers (Chapman 1989; Estrada & Coates-Estrada 1984, 1986, 1991; Julliot 1994, 1996b). Primate species vary in body size, diet, activity rhythm and spatial occupancy; all these parameters affect the pattern of seed dispersal as well as post-dispersal seed fate. Howler monkeys (*Alouatta* spp.) are mostly folivores, but fruit can seasonally represent a large part of the diet (see Julliot & Sabatier

1993 for a review). Their defecations containing large amount of viable seeds, and are concentrated under the sleeping sites of the troops (Andresen 1994, and in press; Julliot 1996a, 1997). The resulting clumped seed distribution is distinct from the scattered one produced by other primates, like the spider monkey (*Ateles* spp.) (Andresen 1994, in press; Zhang & Wang 1995).

The net effect of dispersal by primates on plant recruitment cannot be assessed without taking into account the post-dispersal fate of seeds (Chapman 1989; Price & Jenkins 1986) because predation and secondary seed dispersal can affect the distribution and survival of seeds and seedlings (Forget *et al.* 1998). Rich communities of coprophagous beetles (Scarabaeidae) that use vertebrate dung for food and reproduction, inhabit tropical rain forests (Cambefort 1982, Gill 1991, Halffter & Matthews 1966, Halffter *et al.* 1992, Hanski 1989, Howden & Nealis 1978, Howden & Young 1981). In neotropical forests primate dung represents an abundant resource for dung beetles (Gill 1991). Species of ball-rollers and tunnellers have been observed to relocate and bury seeds contained in monkey dung (Andresen 1994, and in press; Estrada & Coates-Estrada 1986, 1991; Shepherd & Chapman 1998). These authors found a negative relationship between seed size and the proportion of seeds buried, and showed that ball-rolling beetles were less efficient than tunnelling ones. Meanwhile Shepherd & Chapman (1998) showed that larger seeds were buried more shallowly than smaller seeds. While moving seeds both horizontally and vertically, thus reducing clumping of seeds, dung beetles make seeds less detectable to seed predators, therefore enhance seed survival. Moreover, rapid processing of dung by beetles decreases the attractive effect of dung toward rodents (Andresen 1994, and in press; Janzen 1986). All of the dispersal role was attributed to beetles because rodents were considered as purely destructive. However, it is now known from studies conducted in neotropical forests that rodents may also act as secondary dispersers (Forget 1991, 1993; Forget & Milleron 1991; Hallwachs 1994). From now on a comprehensive appraisal of the role of dung beetle as secondary seed dispersers has to take this biotic factor into account.

The objective of this study was to determine the effect of dung beetle size on seed fate, in a forest where the dung beetle community comprises some of the largest neotropical species of Scarabaeinae. The role of selected large ball-rolling and tunnelling species on the rate of seed burial and depth of burial according to seed size was tested. As an example, the effect of burial on germination rates and predation with one of the most commonly dispersed seed species in the study area was analysed.

STUDY SITE AND SPECIES

Study site

The study site is the Nouragues Station in French Guiana (4°5'N, 52°40'W), situated in the middle of a block of continuous rain forest which has been

uninhabited for more than 200 y. The climate is characterized by a long wet season (mid-November to mid-August), irregularly interrupted by a short dry period around March, and a main dry season during the other months. Mean annual rainfall is 2880 mm and temperature ranges 19–36 °C (Cockle 1997).

In the Nouragues area *c.* 1200 woody trees, lianas, palms and herbaceous species were identified (Poncy *et al.* 1998). The most important families of large trees and lianas are Caesalpiniaceae, Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae (Sabatier & Prévost 1990).

Howler monkeys

The red howler monkey, *Alouatta seniculus* Linné 1766, one of the largest primate species in neotropical forests, is the mostly folivorous, although the average fruit consumption in French Guiana ranges from 25 to 46% of total consumption (Guillotin *et al.* 1994, Julliot & Sabatier 1993, Simmen & Sabatier 1996). In the Nouragues area the highest consumption of mature fruit (51% of feeding units per month) was observed during the period of peak fruit production, from February to May (Julliot & Sabatier 1993, Sabatier 1985). Red howlers preferentially consume medium-sized fruits with yellow colour dispersing seeds from fruit with a hard pericarp and/or large seeds (Julliot 1996a).

Dispersed seeds

At the Nouragues Station howler monkeys disseminate the seeds by endozoochory of at least 86 plant species, *i.e.* *c.* 95% of plant species from which they eat ripe fruit (Julliot 1996a). Passage through the digestive tract does not significantly modify the germination success of most plant species (Julliot 1996b). The size of disseminated seeds varies from 1 mm in diameter (*Ficus* spp., Moraceae) to 4 cm × 2.5 cm (*Pouteria laevigata*, Sapotaceae) (Julliot 1996b). During this study period of the seed species (*n* = 47) defecated by howlers, 36% had a diameter 5–10 mm and 49% 10–15 mm. At Nouragues, the Sapotaceae family is dominant in the monkeys' diet by at least 21 dispersed species (Julliot 1996b). Among them, *Chrysophyllum lucentifolium* seeds occurred most frequently in faecal samples (44%), especially because one of the main howler monkey troops exploited an area where this species was abundant (Julliot 1996a, this study). Other seed species used in this study were mostly selected according to their high occurrence in defecations (Table 1). Although *P. laevigata* seeds were not found in dung during the study period, the species was considered all the same because it is known to be the largest seed species howler monkey disperses (Julliot 1996b).

Dung beetle community

Of 57 dung beetle species captured in the Nouragues area with pitfall traps baited with howler monkey dung, 42 were tunnellers which bury the dung at the site of deposition, 10 were rollers which roll dung balls some distance before burying them and the remaining five species were dwellers (*Eurysternus* spp.),

Table 1. Plant species used in experiments with seed dimensions (SE in parentheses) and percentage of occurrence in 100 defecations of howler monkeys (except for *P. laevigata*, see text).

Plant species (Family ¹)	Seed length (mm)	Seed width ² (mm)	N	% in faeces
<i>Pouteria laevigata</i> (Mart.) Radlk. (Sapo.)	45.5 (0.8)	21.8 (0.4)	22	nil
<i>Chrysophyllum lucentifolium</i> Cronq. (Sapo.)	31.4 (0.6)	13.2 (0.3)	15	44
<i>Tetragastris</i> spp (Burs.) ³	17.9 (0.5)	9.1 (0.3)	14	30
<i>Micropholis guianensis</i> (A.DC.) (Sapo.)	14.2 (0.2)	8.2 (0.1)	10	14
<i>Protium</i> sp (Burs.)	15.6 (0.3)	7.7 (0.3)	10	11
<i>Parahancornia fasciculata</i> (Poir.) Benoist (Apoc.)	12.0 (0.2)	6.6 (0.1)	30	12
<i>Doliocarpus</i> sp (Dill.)	7.6 (0.2)	5.7 (0.3)	20	20
<i>Schefflera paraensis</i> Huber ex Ducke (Aral.)	9.0 (0.1)	5.4 (0.1)	15	26
<i>Duguetia</i> sp (Anno.)	7.5 (0.3)	4.3 (0.2)	10	1
<i>Solanum</i> sp (Sola.)	4.1 (0.1)	3.6 (0.1)	15	5

¹Anno., Annonaceae; Apoc., Apocynaceae; Aral., Araliaceae; Burs., Burseraceae; Dill., Dilleniaceae; Sapo., Sapotaceae; Sola., Solanaceae.

²diameter of the short axis for elongated seeds.

³*T. panamensis* (Engl.) Kuntze and *T. altissima* (Aubl.) Swart.

which process the dung right under the dung pad itself (F. Feer, unpubl. data). Large tunnellers (> 12.5 mm) represented 12% of the total number of individuals captured (n = 2417) representing 10 species including the largest species attracted by howler dung, *Sulcophanaeus faunus* (37 mm). All *Dichotomius* spp. (five species) were nocturnal whereas other large tunnellers were diurnal (Table 2). Large ball rollers (> 7 mm) represented 19% of the total number of individuals. Eight species were captured, of which only one was nocturnal (*Canthon bicolor*) which was also the largest roller (12.6 mm). The rolling and tunnelling dung beetle species used in this study, were selected for their large size and/or abundance. All beetles were identified by Y. Cambefort using collections of the Laboratoire d'Entomologie in the Muséum National d'Histoire Naturelle (Paris).

Table 2. Species of dung beetles (except *Eurysternus* spp.) attracted by howler dung at Nouragues Station, their size (based on a minimum n = 11 individuals), activity rhythm and abundance (number of individuals in a total sample of n = 2417).

Species	Mean body length (mm)	Rhythm ¹	Abundance % (SD)
Tunnellers			
<i>Sulcophanaeus faunus</i> (Fabricius, 1775)	37.0	D	†
<i>Dichotomius boreus</i> (Olivier, 1789)	23.7	N	52
<i>Oxysternon festivum</i> (Linné, 1767)	21.0	D	30
<i>Dichotomius subaeneus</i> (Castelnau, 1840)	17.4	N	14
<i>Oxysternon durantoni</i> Arnaud, 1984	16.4	D	140
<i>Dichotomius lucasi</i> (Harold, 1869)	12.5	N	45
Ball-rollers			
<i>Canthon bicolor</i> Castelnau, 1840	12.6	N	51
<i>Canthon semiopacus</i> Harold, 1868	10.2	D	37
<i>Hansreia affinis</i> (Fabricius, 1801)	9.2	D	233

¹D = diurnal, N = nocturnal;

†present but not captured in pitfall traps.

MATERIALS AND METHODS

Primary seed dispersal by howler monkeys

I studied seed dispersal by red howler monkeys in April–May 1995, 1996 and 1997, by collecting faecal samples under sleeping sites of two to three troops. Faecal samples were washed through sieves following guidelines by Julliot & Sabatier (1993). Seeds were identified at least to genus and measured. Diameter or in cases of elongated seeds, the diameter of the short axis, was taken as the most relevant dimension with respect to the animals' ability.

Dung processing by beetles

The dung processing behaviour of beetles was observed for 26 h on the defecation sites during day and night. The removal rate by dung beetles and other coprophagous insects of the howler dung deposited in the morning was evaluated by estimating visually the proportion of dung (in classes of 25, 50, 75 and 100%) which disappeared after 8–10 h and after 24 h. I also made the same observations using 50-g piles of howler dung (see Experiment 1). The differences in removal rate between time and dung quantity was tested with chi-squared and Fisher's exact tests, classes being pooled where necessary.

Seed processing by beetles

Experiment 1. To assess the response of dung beetles to seeds in monkey dung, *c.* 50 g of dung with two to four seeds of three dispersed species (*C. lucenitifolium*, *Tetragastris* sp., *Micropholis guianensis*) were placed simultaneously on the forest floor at 10 random locations. Two types of exclosures made of wire mesh were used. The first, with a 2.7 cm × 2.7 cm mesh, prevented access of vertebrates (rodents) but not of beetles. The second exclosure was covered with an additional covering of fine netting thus preventing access of both vertebrates and invertebrates. The third treatment was without any protection. Clumps were deposited between 09h00–11h00 and checked at evening, 24 h later and after 11–14 d. Differences in seed survival between seed species and treatments were tested with chi-squared tests after pooling the data from 10 locations.

Experiment 2. To assess the effect of seed size and dung beetle size on the proportion of seeds buried and the burial depth, seeds of ten different howler-dispersed species, ranging in size from 3.6 to 21.8 mm (Table 1), were placed with *c.* 30 g of dung in a plastic cylinder filled with soil, following guidelines by Estrada & Coates-Estrada (1991). The number of seeds presented in each trial (1 to 100) depended on seed size. Three seed species of different sizes were presented together in each trial to two to five individuals of the same dung beetle species. Six selected species of tunnellers (Table 2) were tested separately in four to 17 trials each. The cylinder was checked after 24 h to determine the proportion of seeds buried. To measure the burial depth the cylinder was opened. The experiments during which all dung was not processed were not considered in the analyses. The seeds still visible on the surface

or remaining in the soil turned over by insects were not considered as buried. I tested the relationship between the rate of burial and seed size with the Cochran's test for linear trend (SYSTAT 1996). Chi-squared and Fisher's exact tests were used to compare rates of burial. The differences between depth of burial were tested with Kruskal-Wallis one-way analysis of variance and Mann-Whitney U-tests. The relationship between depth and dung beetle species, and between depth and seed size was tested using Spearman's rank correlation coefficient.

Experiment 3. To assess the proportion of seeds incorporated into dung balls by rollers, the beetles were placed in a plastic basin 50 cm in diameter filled with a 4-cm layer of soil and covered with a fine netting. Ten to 50 seeds ranging 3.6–6.6 mm (*Parahancornia fasciculata*, *Schefflera paraensis*, *Solanum* sp.) were presented separately to three species of ball-rollers in two to four trials for each species. Dung balls were retrieved for analysis every 6 h until no dung was left in the basin.

Effect of burial on germination and predation of Chrysophyllum lucentifolium seeds

Experiment 4. To estimate the capacity of buried seeds of *C. lucentifolium* to germinate, seeds were deposited at the bottom of 1-cm-diameter holes and covered with loose soil at five random locations. Five seeds, 15 cm apart, were buried at 5 cm and 10 cm depth on a 1-m × 1-m plot surrounded by 2.7-cm × 2.7-cm wire mesh, preventing access of vertebrates. A non-protected plot was placed adjacent to each experimental plot, to test the ability of rodents to find seeds buried in forest soil. The germination rate of seeds placed on the soil surface was obtained by using 7–23 seeds defecated by howler monkeys installed into exclosures on 10 random locations. The experiments were checked weekly to count emerging seedlings. After 6 wk it was considered that all seeds which could emerge had germinated. The differences between germination rates of buried and unburied seeds and between depth treatments, for the pooled data sets, was tested with chi-squared tests.

RESULTS

Dung processing by beetles

During the day, 5–18 individuals belonging to two to six large species of dung beetles arrived on the dung within the first hour after dung deposition. The most abundant and conspicuous tunneller was *Oxysternon durantoni*. Like other Phanaenini (Halffter & Matthews 1966) they rapidly dig a tunnel close to the faecal clump before dragging pieces of dung into it. The largest species, *Sulcophanaeus faunus*, digs tunnels 3 cm in diameter. I occasionally observed *Oxysternon festivum* pushing away dung clumps larger than their body to about 1 m distance. The first dung beetles attracted to dung piles arrived within 1 min. After *c.* 7 min the first ball-roller left the site with a dung ball. *Canthon semiopacus*, one of the most frequent species, make balls of 1.0 cm in diameter. At

Table 3. Dung disappearance of 50-g dung clumps and defecation of red howler, 8–10 h and 24 h after deposition, as numbers of observations in percent disappearance classes.

	Percent of disappearance			
	0–25	26–50	51–75	76–100
50-g dung clumps (n = 20)				
After 8–10 h	9	1	3	7
24 h	1	0	2	17
Howler defecations (n = 13)				
After 8–10 h	4	0	2	7
24 h	0	0	1	12

night the ball roller *Canthon bicolor* was the first one to come on the dung followed by *Dichotomius boreus*, the species most abundant and important in terms of biomass.

The dung relocation and burying activity of diurnal beetles showed great variability between sites (Table 3). The dung removal after 24 h showed that nocturnal beetles exploited most of the dung that was not removed during the day. Although large quantities of dung were present in the morning under sleeping sites (300 to 800 g fresh weight), there were no significant differences in the disappearance rates when compared with the small faecal clump in the evening ($\chi^2 = 2.69$, $df = 2$, $P > 0.05$) and after 24 h (Fisher's exact test, $P > 0.05$).

Seed processing by beetles

Experiment 1. Dung beetles were active on all sites, unexclosed or equipped with semipermeable exclosure. Additionally, tunnellers were able to process the dung inside most of the control exclosures by digging from outside the cage. After 11–14 d more seeds of the studied species were left on the soil surface in the semipermeable exclosure than in the unexclosed condition (all χ^2 values between 15.2 and 35.3, $df = 1$, $P < 0.001$; Table 4). In the semipermeable experiment 13–23% of seeds were buried apparently by dung beetles. On non-protected sites, only 7–10% of seeds survived, showing high removal and consumption rates by rodents or other terrestrial vertebrates. Four out of seven *Tetragastris* seeds not touched by vertebrates germinated whilst the others died. The proportion of seeds left on the surface by dung beetles was not significantly different between the three species. There was no difference in proportion of

Table 4. Proportion of *Chrysophyllum lucentifolium* (13.2 mm), *Tetragastris* sp. (9.1 mm) and *Micropholis guianensis* (8.2 mm) seeds left on the ground in unexclosed, semipermeable and exclosed conditions after 11–14 d. Number of seeds in parentheses. Within lines, different letters indicate which were significantly different (χ^2 tests, $P < 0.05$).

Seed species	Unexclosed	Semipermeable	Exclosed
<i>Chrysophyllum</i>	10.0 (30) ^a	86.7 (30) ^b	86.7 (30) ^b
<i>Tetragastris</i>	26.9 (26) ^a	80.8 (26) ^b	88.9 (18) ^b
<i>Micropholis</i>	6.7 (30) ^a	76.5 (34) ^b	78.8 (33) ^b

seeds left on the soil surface between the semipermeable exclosures and the control accidentally exposed to tunnelling dung beetles.

Experiment 2. In the plastic cylinder the proportion of buried seeds decreased as the size of seed increased for *S. faunus*, *D. boreus* and *O. durantoni* ($\chi^2 = 4.68$, 78.23 and 74.05, $df = 1$, $P = 0.03$, $P < 0.001$ and $P < 0.001$ respectively) (Figure 1). Experiments with *O. festivum*, using seeds of *Doliocarpus* sp. and *C. lucentifolium* showed a similar trend (Cochran's test; $\chi^2 = 35.93$, $df = 1$, $P < 0.001$) whereas no differences were detected for *Dichotomius subaeneus* and *Dichotomius lucasi* (Fisher's exact test, $P > 0.05$). Small *Doliocarpus* seeds (5.7 mm) were buried at high rates by all beetle species except *D. subaeneus* and *D. lucasi*. The proportion of buried *C. lucentifolium* seeds increased as the size of dung beetle increased from *O. durantoni* to *S. faunus* (Cochran's test; $\chi^2 = 36.45$, $df = 1$, $P < 0.001$). Large beetle species such as *S. faunus* and *D. boreus*, buried 68 and 46% of *C. lucentifolium* seeds respectively whereas *O. durantoni* and smaller species had low effect on seeds ≥ 7 mm. *S. faunus* buried 30% of the large *Pouteria laevigata* seeds whereas *D. boreus* was observed to leave on the surface all seeds out of three of this species.

The seeds were buried at average depths ranging from 2 to 28 cm, depending on dung beetle species. The depths were significantly different between seed species for *S. faunus*, *D. boreus* and *O. durantoni* (Table 5, all $P < 0.05$). The correlation coefficients (r_s) between seed size and depth for *S. faunus* and *O. durantoni*, were 0.06, and 0.20 respectively. Only *D. boreus* showed burial depths significantly negatively correlated to the seed size ($r_s = -0.53$, $P < 0.0005$). Compared to *S. faunus*, *D. boreus* dragged small *Doliocarpus* seeds to larger depths (Mann-Whitney; $U = 1141$, $P < 0.001$) and buried large *C. lucentifolium* seeds less deep (Mann-Whitney; $U = 42$, $P < 0.001$). The burial depths of *Doliocarpus* seeds were significantly different between beetle species (Kruskal-Wallis; $H = 148$, $df = 5$, $P < 0.0005$). Paired-tests were all significant ($P < 0.01$), except between *O. durantoni* and *S. faunus* ($P > 0.05$). Diurnal species showed intermediate depth level between nocturnal species like *D. boreus* (28 cm) and *D. subaeneus* and *D. lucasi* (5 and 2 cm, respectively).

Experiment 3. The percentage of *Solanum* seeds included in dung-balls varied significantly with species of roller ($\chi^2 = 26.17$, $df = 2$, $P < 0.001$). The largest species, *C. bicolor*, included 20% ($n = 100$) of the *Solanum* seeds. *Hansreia affinis* and *Canthon semiopacus*, which are similar in size, included 44% ($n = 100$) and 8% ($n = 50$) of the *Solanum* seeds respectively. This suggested that important specific differences in incorporating seeds in balls may exist among rollers. Larger seeds such as *S. paraensis* (5.4 mm) were only taken by *H. affinis* (one out of 10), while all the slightly larger seeds of *Doliocarpus* (5.7 mm) were rejected.

Effect of burial on germination and predation of Chrysophyllum lucentifolium seeds

Experiment 4. Burial of *C. lucentifolium* seeds showed that the proportion of germinating seeds was not different between burial depths, and between protected and unprotected sites (Table 6). Total average germination rate (34%,

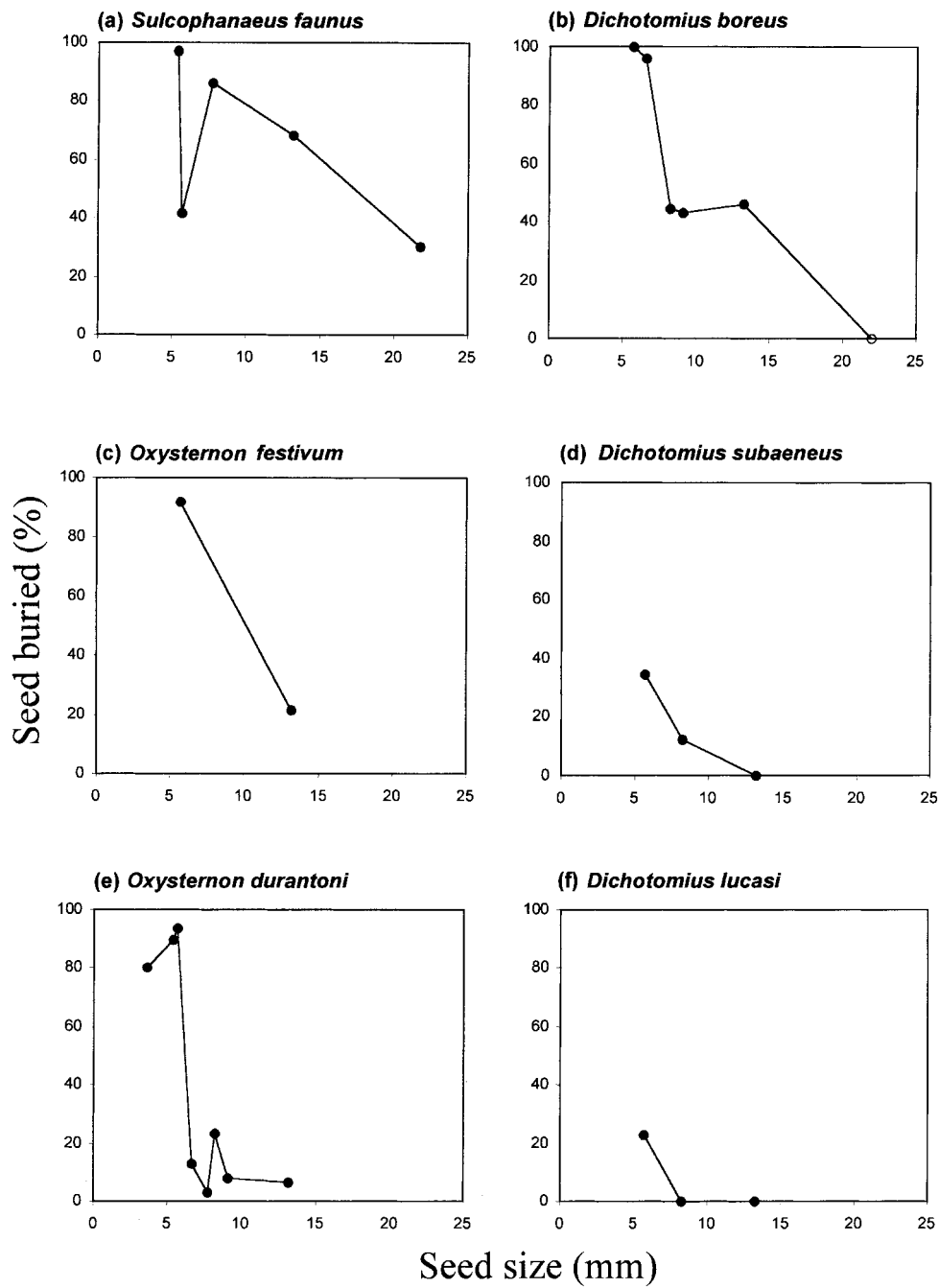


Figure 1. Relationship between seed size and percentage of seeds buried by dung beetles (tunnellers) arranged in order of decreasing beetle size (a) to (f) (see Table 2). The empty symbol with *D. boreus* corresponds to three *P. laevigata* seeds, not considered in the statistical analysis.

Table 5. Burial depths (cm) of seeds by tunnelling dung beetles (arranged in order of decreasing size—see Table 2) in plastic cylinder experiments. SEs in parentheses.

Seed species	Seed size (mm)	Dung beetle species ¹					
		S. f. ²	D.b. ³	O.f.	D.s.	O.d. ⁴	D.l.
<i>Chrysophyllum</i>	13.2	15.7(1.4)	6.4(1.1)				
<i>Micropholis</i>	8.2		11.6(2.0)				
<i>Protium</i>	7.7	20.3(1.5)					
<i>Parahancornia</i>	6.6		27.6(0.4)				
<i>Doliocarpus</i> ⁵	5.7	14.6(1.1)	28.0(0.9)	20.3(0.7)	5.0(0.8)	12.5(1.3)	2.0(0.4)
<i>Schefflera</i>	5.4	18.2(0.7)				9.9(1.1)	
<i>Duguetia</i>	4.3					14.7(0.9)	
<i>Solanum</i>	3.6					13.5(0.5)	
Mean		16.7(0.6)	24.6(0.9)			12.0(0.7)	

¹Dung beetle species: S. f. = *Sulcophanaeus faunus*; D. b. = *Dichotomius boreus*; O. f. = *Oxysternon festivum*; D. s. = *Dichotomius subaeneus*; O. d. = *Oxysternon durantoni*; D. l. = *Dichotomius lucasi*.

Depth differences between seed species (Kruskal-Wallis test): ²S.f., $H = 14.86$, $df = 3$, $P = 0.002$; ³D.b., $H = 50.36$, $df = 3$, $P < 0.0005$; ⁴O.d., $H = 9.12$, $df = 3$, $P = 0.028$.

⁵Depth differences between beetle species for *Doliocarpus* (Kruskal-Wallis test): $H = 148.05$, $df = 5$, $P < 0.0005$.

Table 6. Percentages of *Chrysophyllum lucentifolium* seeds germinating and established out of a total of 25 seeds (five seeds \times five sites) buried at 5- and 10-cm depths after 6 wk.

Depth (cm)	Not protected		Protected	
	5	10	5	10
Germination	36	24	44	32
Establishment	8	8	40	32

$n = 100$) was significantly lower than the germination rate of protected defecated *C. lucentifolium* seeds (93.5%, $n = 123$, $\chi^2 = 88.1$, $df = 1$, $P < 0.001$). Mammals did not dig up buried seeds, but gnawed the germinating seedlings as soon as the white stems emerge. This resulted in a significantly lower proportion of established seedlings on unprotected sites at 5 and 10 cm depth than at protected sites ($\chi^2 = 7.01$, $df = 1$, $P < 0.01$ and $\chi^2 = 4.50$, $df = 1$, $P < 0.05$ respectively).

DISCUSSION

Howler monkeys are important dung producers in the neotropical rainforest. At Nouragues Station, Julliot (1996b) estimated that a troop of six to eight individuals collectively defecated an average of 1.5 kg fresh weight of faeces per day. An estimation based on home range data gave 55 g $ha^{-1} d^{-1}$ which is very close to the 54 g given by Gill (1991) in BCI, Panama, but much higher than the 11 g cited by Estrada *et al.* (1993) for Los Tuxtlas in Mexico. My observations of dung removal under sleeping sites, where 61% of defecations occurred (Julliot 1996b), suggested that diurnal dung beetles were able to process large amounts of dung rapidly, as shown also by Estrada & Coates-Estrada (1991) and Peck & Forsyth (1982). Nevertheless, in some sites, dung is still

available for nocturnal dung beetles, probably because the foraging activity and distribution of diurnal dung beetle species is not uniform. Moreover, defecation rhythm of howler monkeys is bimodal (Julliot 1996b), and a larger proportion of dung produced during the afternoon is likely to be exploited by nocturnal dung beetles than of morning dung. The importance of nocturnal species in processing the dung of diurnal frugivore mammals as howler monkey and coati, was also suggested by the data of Estrada *et al.* (1993).

The rate of burial of seeds was shown to be inversely correlated with seed size for three large tunnellers. When pooled together my data offer a similar trend to that of the studies of Estrada & Coates-Estrada (1991), Shepherd & Chapman (1998), and Andresen (1994). According to all of the available data, a high percentage of seeds not >5 mm are buried by dung beetles. My experiments showed that the highly variable rate of burial observed for larger seeds was related to dung beetle size as well as to seed size. For example, the largest tunneller measuring 37 mm in length was able to bury 68% of *C. lucentifolium* seeds whereas beetles species < 21 mm had almost no effect on them. The field experiment with this seed species showed a rate of burial of only 13%, which can be explained by the rarity of a large-sized beetle such as *S. faunus*, and by the fact that small amounts of dung were likely to attract fewer individuals and smaller species (see Peck & Forsyth 1982).

Similar to other studies, I also observed that ball-rolling beetles processed fewer seeds and smaller ones, compared to tunnelling beetles. This is most likely to be an effect of dung beetle size as rollers are smaller than tunnellers in all Scarabaeidae communities of tropical forests (Hanski 1989, Hanski & Cambefort 1991). The ratio of the weight of the provisioned dung to the size of the beetle is smaller for ball-rolling species compared to tunnelling species (Hanski & Cambefort 1991). It is therefore possible that ball rollers must be more selective when making their dung ball and avoid incorporating in it nonpalatable and voluminous seeds.

Tunnellers (except two *Dichotomius* spp.) buried seeds to an average depth > 12 cm. My experimental data are consistent with the field observations of Halfpeter & Matthews (1966) on the structure of burrows of *Phanaeus* and *Dichotomius* spp., and contrast very much with depth of burial recorded by Estrada & Coates-Estrada (1991), which were rarely >12 cm. This may be related to the small size of the dung beetle species present in the Mexican forest of Los Tuxtlas, and emphasizes the importance of the size structure of the dung beetle community in many aspects of seed fate.

C. lucentifolium seeds buried >5 cm deep were protected from predators. Andresen (1994, and in press), Shepherd & Chapman (1998), and Estrada & Coates-Estrada (1991) similarly showed that burial makes seeds less detectable. Similarly to these authors I observed high rates of removal and predation among seeds that were left above soil surface (e.g., for *C. lucentifolium* 38% and 29%, removal and predation, respectively). Furthermore, Andresen (1994)

showed that fresh dung attached to seeds is an olfactory attractant for rodents (see also Janzen 1982). By rapidly removing dung matter, beetles shorten the duration of such an effect.

In agreement with results of Shepherd & Chapman (1998), I observed that experimental burial has a negative effect on germination success of *C. lucentifolium* seeds even when seeds were deposited at lower depths than those originated by the dung beetles. Moreover, I assume that the energy spent by the emerging seedling to grow from a deep-buried seed may be disadvantageous for the plant species. Shepherd & Chapman (1998) postulated a theoretical optimum depth for a seed species given that, with increasing burial depth, the probability of seed escaping predation increases, and the probability of a seedling emerging decreases. The very small dormant seeds (e.g. of Moraceae, Cecropiaceae) which are buried at high rates by all dung beetles, are efficiently incorporated into the soil seed-bank, and may later germinate (de Foresta & Prévost 1986). Some proportion of small or medium-sized non-dormant seeds may serendipitously benefit from dung beetles' burying activity. However, this study suggests that the effect on the probability of seed survival is likely to vary with the tribes of the species of tunnellers (e.g. nocturnal *vs.* diurnal). Consequently the timing of dung deposition may be of some importance given the rapidity of dung beetles' action.

The monitoring of seed fate has shown that secondary dispersal by rodents is more common than previously thought (see Asquith *et al.* 1997, Forget *et al.* 1998 for a review). Large dasyproctids but also small echimyid rodents such as spiny rats are important scatterhoarders of seeds of a wide range of sizes (Forget 1990, 1996; Forget & Milleron 1991; Forget *et al.* 1998; F. Feer, unpubl. data). Studies conducted in Panama (Forget *et al.* 1998) and Costa Rica (Hallwachs 1994) showed that caching rates tend to increase with seed weight. A similar relationship seems to exist in French Guiana (F. Feer, unpubl. data) resulting in a growing importance of rodents as secondary dispersers when seed size increases. There is thus probably an opposite gradient of effect on seed survival of rodents and dung beetles in relationship with seed size. Their respective and interactive net effects on seed fate are nevertheless difficult to assess, given the numerous other biotic and abiotic factors involved. Thorough case studies would be useful to unravel the complex interventions of multiple and independent animal groups involved in the process of forest regeneration.

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